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> de la SOCIÉTÉ SUISSE DE ZOOLOGIE et du MUSÉUM D'HISTOIRE NATURELLE de la Ville de Genève

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ZOOLOGIE

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TOME 119—FASCICULE 4

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Description of a new species of the genus *Fessonia* (Acari: Prostigmata: Smarididae) from Iran

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Description of a new species of the genus *Fessonia* (Acari: Prostigmata: Smarididae) from Iran. - *Fessonia torshizica* Salarzehi & Hajiqanbar n. sp. is described from larvae collected in the soil of vineyards in northeastern Iran. This is the second species currently known from larvae in the genus *Fessonia*. Some morphological characters of the new species are compared with its only congener, *F. papillosa* (Hermann 1804).

Keywords: Parasitengona - Trombidiformes - Erythraeoidea - larva - *Fessonia torshizica*.

INTRODUCTION

Mites of the cohort Parasitengona (Acari: Trombidiformes) are a large and diverse group of prostigmatic mites distributed worldwide. These mites usually parasitize invertebrates during their larval stage but the deutonymphs and adults are predaceous. The superfamily Erythraeoidea is one of the largest parasitengone superfamilies, consisting of two families: Smarididae and Erythraeidae. The family Smarididae, with 10 genera and 53 species (Zhang *et al.*, 2011), is a relatively small family usually found in grassland and litter or under the bark of trees (Southcott, 1996; Krantz & Walter, 2009).

Mites of the family Smarididae are classified in two subfamilies, Smaridinae and Hirstiosomatinae, the former with five genera including *Fessonia* von Heyden, 1826. This genus is distributed in Europe, Australia, North America, Asia and Africa, and hitherto encompassed 10 known species, nine of which were described from adults. Previously the larval stage of only one species, *F. papillosa* (Hermann 1804) from France, Italy, Croatia, Germany, Greece and Hungary was known (Wohltmann, 2010). During a faunistic survey of mites in vineyards of Kashmar and Torshiz counties (northeastern Iran) in 2010-2011, we found in soil samples larvae of a species of *Fessonia* which is new to science. This is the first record of the genus *Fessonia* from Iran. In the following we describe this new species and compare its morphological characters with those of the larva of *F. papillosa*. We consider it very unlikely that the larvae of the new species are conspecific with adults of any of the previously described *Fessonia* species.

MATERIALS AND METHODS

The mite specimens were collected from litter and soil samples and extracted by Berlese funnel, then cleared in lactophenol and mounted in Hoyer's medium. The morphology of the specimens was studied with an Olympus BX51 equipped with phase contrast and a drawing tube. All measurements in this description are given in micrometres. In the description, body measurements are given for the holotype and the paratype, the latter in parentheses. Terminology and abbreviations follow those of Grandjean (1947) and Wohltmann (2010).

The holotype of the new species is deposited in the Acarological Collection, Zoological Museum, College of Agriculture, University of Tehran, Karaj, Iran. The paratype is deposited at the Natural History Museum of Geneva, Switzerland.

The following abbreviations are used in the description: ϵ (famulus) = specialized smooth seta on tarsus of leg I, usually small; ζ (eupathidium) = specialized smooth seta on legs and palp, in particular on tarsus; z (accessory seta) = smaller seta close to dorsal eupathidium on tarsus of leg I; κ (kappa) = microseta on tibia and genu of walking legs; σ (sigma) = solenidion on genu; φ (phi) = solenidion on tibia; ω (omega) = solenidion on tarsus; I = first walking leg; II = second walking leg; III = third walking leg; AL = first pair of non-sensillary setae on scutum in larvae; ASens = first pair of trichobothria on scutum in larvae; as (oral seta) = located anteriorly on gnathosoma; Bf = basifemur; bs (subcapitular seta) = located ventrally on gnathosoma; cs (adoral seta) = usually small smooth pointed setae located dorsally on gnathosoma; Cx (coxa) = epimeral plate; Fe = femur; fn = number of setae; Ge = genu; IP (index pedal) = sum of all lengths of legs; N = non-specialized seta on palp and legs; PL = second pair of nonsensillary setae on scutum in larvae; PSens = second pair of trichobothria on scutum in larvae; Ta = tarsus; Tf = telofemur; Ti = tibia; Tr = trochanter.

SYSTEMATIC ACCOUNT

Family Smarididae Vitzthum, 1929 Genus *Fessonia* von Heyden, 1826

Fessonia torshizica Salarzehi & Hajiqanbar n. sp.

Figs 1-7

MATERIAL STUDIED: Holotype larva (SS-2010-1a), free-living, collected from soil samples of vineyards in Torshiz, Khorasan Razavi province, Northeastern Iran, 35° 11' N, 58° 72' E, 1215 m. a.s.l. 24-IX-2010, leg. S. Salarzehi. Paratype: 1 larva (SS-2010-1b), same collection data as for holotype.

ETYMOLOGY: The specific epithet refers to the type locality, Torshiz.

DIAGNOSIS: Tarsus 1 with 26 serrate setae; genu I without microseta (k); genua I, II, and III each with one solenidion (σ); basifemur I and telofemur I with 3 and 4 serrate setae, respectively; tarsus II with 24 serrate setae.

DESCRIPTION OF LARVA: Metric data given in Table 1.

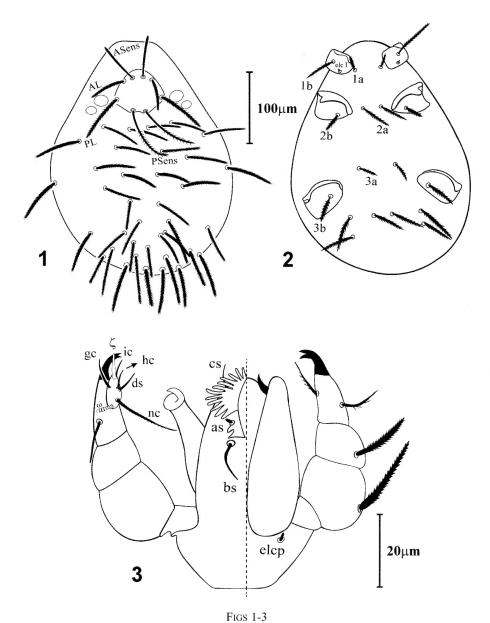
Idiosoma (Figs 1-2). Length 316 (300), width 249 (221). Dorsal scutum subpentagonal, anterior border curved, with two pairs of barbed normal setae (AL, PL), two pairs of trichobothria (ASens, PSens), ASens almost setulose throughout but PSens setulose only in posterior half. Laterally of scutum two pairs of eyes. Remaining part of dorsum carrying 38 barbed setae in rows C-H. Venter with all setae barbed except elc I. Coxa I with setae 1b 52 (49) and 1a 19 (18), setae 1a located outside, close to

TABLE 1. Morphometric data of larvae of Fessonia torshizica n. sp.

Character	Holotype	Paratype	
	61	58	
Scutum lenght Scutum width	65	61	
ASens	53	47	
ASens-ASens	33 16	15	
PSens	84	77	
PSens-PSens	19	18	
AL	47	39	
AL AL-AL	44	37	
PL	68	61	
	65	55	
PL-PL		33 7	
Palpal Tr	8		
Palpal Fe	21	20	
Palpal Ge	11	10	
Palpal Ti	14	12	
Odontus	10	8	
Palpal Ta	8	8	
Cx I	25	21	
Tr I	19	13	
BfI	28	22	
Tf I	22	21	
Ge I	31	26	
Ti I	42	38	
Ta I	39	31	
Leg I	208	172	
Cx II	35	23	
Tr II	22	14	
Bf II	26	21	
Tf II	22	19	
Ge II	29	28	
Ti II	38	34	
Ta II	34	31	
Leg II	203	171	
Cx III	36	26	
Tr III	22	19	
Bf III	27	22	
Tf III	30	25	
Ge III	33	32	
Ti III	59	55	
Ta III	40	35	
Leg III	248	215	
IP	659	558	

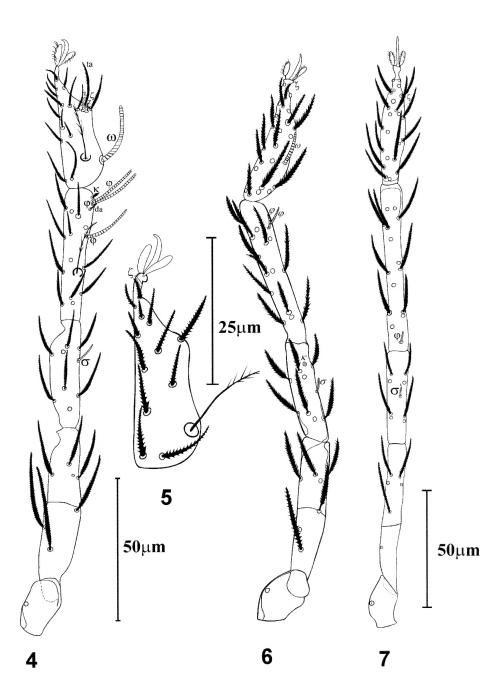
margins of coxae I. Setae 2b 21 (19), situated on coxae II; setae 2a 44 (41), situated between coxae II. Setae 3b 35 (32), situated on coxae III; setae 3a 24 (22), situated anteriorly outside coxae III. Three pairs of setae situated posterior to coxae III.

Gnathosoma (Fig. 3). Chelicera with cheliceral base 60 (64) long and with smooth movable claw; cheliceral digits short, 5 (4) long. Dorsal gnathosoma with a pair of smooth, pointed adoral setae *cs* 6 (5) anteriorly and with a pair of short, thick and blunt supracoxal setae *elcp* 3 (2) in lateral position. Ventrally a pair of smooth and pointed subcapitular (tritorostral) setae *bs* 10 (8) and a pair of short, thick and blunt



Fessonia torshizica n. sp., larval holotype. (1) Dorsal view of idiosoma. (2) Ventral view of idiosoma. (3) Dorsal view (right side) and ventral view (left side) of gnathosoma.

oral setae as 3 (2). Palpal femur with one barbed dorsal seta, 21 (19) long, palpal genu with one barbed dorsal seta, 11 (9) long. Palpal tibia with one smooth and two barbed setae. Odontus bifid, 9 (7) long. Palpal tarsus with four smooth setae gc 7 (6), ds 5 (4), ic 4 (3), hc 3 (2), one barbed seta nc 15 (14), one solenidion (ω) and one prominent distal eupathidium (ζ).



FIGS 4-7
Fessonia torshizica n. sp., legs of larval holotype. (4) Dorsal view of entire leg I. (5) Ventral view of tarsus of leg I. (6-7) Dorsal view of entire legs II and III.

$\begin{array}{cccccccccccccccccccccccccccccccccccc$	0 N
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	0.14
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 N
Palpal Ta $5 N, 1 \xi, 1 \omega$ $5 N, 1 \xi, 1 \omega$ Cx I $1 N, 1 \text{ elc}$ $1 N, 1 \text{ elc}$ Tr I $1 N, 1 \text{ elc}$ $1 N, 1 \text{ elc}$ Tr I $1 N, 1 \text{ elc}$ $1 N, 1 \text{ elc}$ Bf I $3 N, 1 \text{ elc}$ $8 N, 1 \text{ elc}$ Ge I $8 N, 1 \sigma$ $8 N, 1 \sigma$ Ti I $13 N, 3 \varphi, 1 \text{ da}, 1 \kappa, 1 \text{ tr}$ $13 N, 3 \varphi, 1 \text{ da}, 1 \kappa, 1 \text{ tr}$ Ta I $26 N, 2 \xi, 1 Z, 1 \omega, 1 \epsilon, 1 \text{ ta}, 1 X, 2 \text{ tr}$ 20 - $22 N, 2 m, 2 m, 2 m, 2 m, 2 m, 2 m, 2 m,$	1 N
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3 N
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1 ζ, 1 ω
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	I, 1 elc
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1 N
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2 N
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5 N
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1 σ, 1 κ
Cx II 1 N Tr II I N Bf II 2 N Tf II 5 N	1 da, 1 κ, 1 tr
Cx II	ζ , 1 Z, 1 ω , 1 ϵ ,
Tr II IN Bf II 2 N Tf II 5 N	1 X, 2 tr
Bf II 2 N Tf II 5 N	1 N
Tf II 5 N	1 N
	2 N
	5 N
Ge II $8 \text{ N}, 1 \text{ K}, 1 \sigma$ $8 \text{ N},$	1 κ, 1 σ
Ti II 14 N, 2 φ 14	Ν, 2 φ
Ta II 24 N, 1 ζ , 1 ω 21-22 1	Ν, 1 ζ, 1 ω
Cx III 1 N	1 N
Tr III 1 N	1 N
Bf III 1 N	1 N
Tf III 5 N	5 N
Ge III 8 N. 1 σ	8 N
Ti III 14 N, 1 φ 14	Ν, 1 φ
Ta III 23 N, 1 ξ 21-2	3 N, 1 ζ

TABLE 2. Leg chaetotaxy of larvae of Fessonia torshizing n. sp. and F. napillosa

Legs (Figs 4-7). Leg I 208 (172) long, femora I-III divided into basi- and telofemur; segmentation formula: 7-7-7. Details of leg chaetotaxy in Table 2. Trichobothria present on tibia and tarsus of leg I. Anterior trichobothrial sensilum (ta) on tarsus I forming a complex with spatulate seta (χ) , microsolenidion (ε) , eupathidium (ζ) and seta z. Two trichobothria also located in proximal half of tarsus I. Tibia I with one trichobothrium in proximal half; shape of all trichobothria on leg I similar, with nude base and setulose upper half. A posterior solenidion on tibia I along with seta da. Solenidion (σ) on genu I shorter than 1/2 length of other solenidia on leg I. Leg II 203 (171) long, anterior solenidion on tibia II longer than posterior one. Genu II with only pit of microseta κ present. Solenidion (σ) on genu II subequal to posterior solenidion (φ) of tibia I. Leg III 248 (215) long, solenidion (σ) on genu III a little longer than solenidion (φ) on tibia III. All tarsi I-III with smooth and claw-like empodia; lateral claws pad-like, with small barbs.

REMARKS: Fessonia torshizica n. sp. differs from F. papillosa in fnBf I (3 vs 2), fnTf I (4 vs 5), number of microsetae κ on genu I (0 vs 1), fnTa I (26 vs 20-22), fnTa II (24 vs 21-22), number of solenidia on genu III (1 vs 0) and fnTa III (23 vs 21-23). All leg chaetotaxy characters of the larvae of Fessonia torshizica n. sp. and F. papil losa are compared in Table 2.

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A new species of *Ceratophysella* from Peru (Collembola: Hypogastruridae)

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A new species of *Ceratophysella* from Peru (Collembola: Hypogastruridae). - *Ceratophysella tupamara* sp. nov. from Iquitos, Peru is described and illustrated. It is easy to distinguish from *Ceratophysella denticulata* (Bagnall, 1941), the only species of the genus previously cited from Peru, by its trilobed apical bulb of antennal segment IV, the number of unguicular teeth and the body chaetotaxy.

Keywords: Iquitos - taxonomy - morphology - chaetotaxy.

INTRODUCTION

The genus *Ceratophysella* is distributed worldwide, and represented by more than 130 species (Bellinger *et al.*, 2011) mainly in the Holarctic Region. From South America only three taxa are known: *C. denticulata* (Bagnall, 1941), *C. armata* (Nicolet, 1841) and *C. communis* (Folsom, 1897). Collembola samples from the Museum of Natural History of Geneva were provided to us for study. In that important collection there are several genera from many localities in South America (Palacios-Vargas *et al.*, 2011). Among them we found some specimens of *Ceratophysella* from Peru that belong to a new species which is described in here.

MATERIAL AND METHODS

The description of the new species is based on material from the collection of the Muséum d'histoire naturelle de Genève (Palacios-Vargas *et al.*, 2011). The specimens were first cleared in 10% KOH, then in lactophenol, and mounted on microscopic slides in Hoyer's solution. Drawings were done with a Carl Zeiss contrast microscope, using a drawing tube.

The type material is deposited in the Muséum d'histoire naturelle de Genève (MHNG), and at the senior author's institution, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM).

The terminology follows mainly Fjellberg (1998). Abbreviations are: Abd. = abdominal segment; Ant. = antennal segment; ar = anterior row; bm = basimedial; bl = basilateral; plb = proximal basilateral; mr = middle row; Oc. = ocular setae; Th. = thoracic segment; ss = sensilla; PAO = postantenal organ; pr = posterior row; px = proximal.

RESULTS

Ceratophysella Börner, 1932

Type species: Podura armata Nicolet, 1841

DIAGNOSIS: Well pigmented Hypogastruridae of medium size. Setae differentiated in smooth microsetae or barbulate macrosetae. Seta m2 on Th. II usually absent. Chaetotaxy of type "A" or "B". Anal spines strong and on anal papillae. 8+8 eyes present. PAO with 4 lobes, the anterior lobes larger, about twice the size of one ommatidium. Ant. IV usually with simple apical bulb and 4-8 dorsal sensilla, ventrally with or without sensory file. Between Ant. III and IV often an eversible sac present. The tenent hairs almost always acuminate. Ungues with inner tooth and up to two lateral teeth on each side. Empodial appendix with broad basal lamella and terminal filament reaching half the inner edge of ungues. Ventral tube with 4+4 setae. Retinaculum with 4+4 teeth. Furcula well developed, dens with 6-7 posterior setae. Mucro spoon-shaped, with a high triangular flap on outer lamella.

Ceratophysella tupamara sp. nov.

Figs 1-7

HOLOTYPE: MNHG, without registration number; 1 $\,^{\circ}$ Peru, Department of Loreto, Iquitos, Río Yanayacú; sample of soil between the bark of a tree and the trunk; 18-X-1980; sample PE-80/8; leg. C. Vaucher.

PARATYPES: MNHG, without registration number 1 juvenile; same locality and date as holotype.- UNAM, without registration number; $1\ \delta$, 1 juvenile; same locality and date as holotype.

DESCRIPTION: Maximum body length: up to 1.5 mm. Body granules fine and uniform, dorsal of Abd. V with 10-14 granules between p1 setae. Color: dark blue. Tergite setae of different lengths, some barbulate macrosetae (50-90 μ m), others smooth microsetae (22-50 μ m), besides the sensorial setae (42-50 μ m) (Fig. 1).

Head: Dorsal cephalic chaetotaxy (after Yosii, 1960), see Fig. 1. Differentiation between microsetae and macrosetae clear. Eyes 8+8. Eye patch with 3 setae, Oc₂ longer than Oc₁ and Oc₃, the last two subequal (Fig. 1). Antennae as long as head. Ant. I with 7 setae. Ant. II with 13 setae. Ant. III organ with 2 short rods in a small integumentary fold and 2 guard setae of similar size; eversible antennal sac between Ant. III and Ant. IV present. Ant. IV with trilobed subapical bulb and 7 short, weakly differentiated sensilla (Fig. 2), one microsensillum and one subapical organ. Ventral file organ with about 10 setae. Postantennal organ composed of 4 lobes, about two times as large as the nearest eye, with accessory tubercle (Fig. 1). Labrum with 4 distinct round papillae on distal edge; labral setal formula 4/5, 5, 4. Ventral cephalic chaetotaxy (after Fjellberg, 1998) with 5 setae in px, 4 in bm, 5 in bl, and 3 in plb. Maxilla tullberg-type. Outer maxillary lobe with 2 sublobal setae.

Dorsal thoracic chaetotaxy as in Fig. 1, Th. I with 3+3 dorsal setae in mr (m2 absent) and one lateral. Th. II with 3 rows of setae, m_2 absent, m_6 and p_4 developed as sensorial setae. Th. III with 3 rows of setae: 6+6 setae in ar, 4+4 setae in mr, m_2 present, m_6 developed as sensorial setae; 6+6 setae in pr, p_4 developed as sensilla. Unguis with 1 small inner tooth at 1/2 distance of its inner edge from base, and one lateral tooth 1/4 from base. Basal unguicular lamella broad, with tip of apical filament reaching 1/2 distance of inner edge of unguis. Tibiotarsi I-III each with 1 acuminate tenent hair

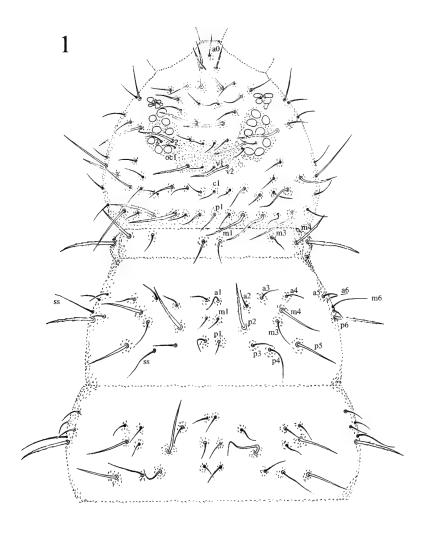
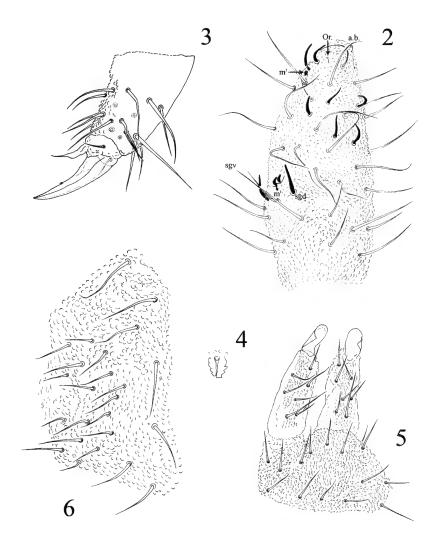


Fig. 1

Cetatophysella tupamara sp. nov., \$\begin{aligned} \text{holotype. Dorsal chaetotaxy of head and thorax.} \end{aligned}

(Fig. 3). Leg III with 3 setae on subcoxa 1, 3 setae on subcoxa 2, 7 setae on coxa, 7 setae on trochanter, 12 setae on femur, 18 setae on tibiotarsus including the acuminate tenent hair (Fig. 3).

Abdominal dorsal chaetotaxy (see Fig. 7) of type "A", after Thibaud *et al.* (2004). Abd. I-III with 2 rows of setae, 8+8 setae in ar, and also in pr, p_5 developed as sensilla. Abd. IV with 3 rows of setae, p_5 developed as sensilla, ratio between length of p_5 (s) and length of $p_6 = 2.0$: 1. Abd. V with 2 rows of setae, 5+5 setae in ar and rp, p_3 developed as sensilla. Abd. VI with 2 rows of setae, 3+3 setae in ar; p_1 replaced by two anal spines, p_2 seta barbulate and long (Fig. 7). Ventral tube short, with 4+4 setae.



Figs 2-6

Cetatophysella tupamara sp. nov., ♀ holotype. (2) Dorsal chaetotaxy of Ant. III and IV. (3) Tibiotarsus III. (4) Tenaculum. (5) Furcula. (6) Genital plate.

Tenaculum with 4 teeth on each ramus, no seta on corpus (Fig. 4). Manubrium with 16 setae; dens with 7 thin setae, one basal seta longer than the others. Mucro slightly spoon-like, with outer lamellae, its apex rounded (Fig. 5); ratio between length of dens and length of mucro = 3.2-3.6: 1. Genital plate of female with 3+3 pregenital setae, 15 circumgenital setae and 2 eugenital (Fig. 6), genital plate of male with 3+3 pregenital setae, 13 circumgenital and 4+4 eugenital. Anal lobes with 19 setae each. Two anal spines on Abd. VI short and curved, longer than their basal papillae (Fig. 7).

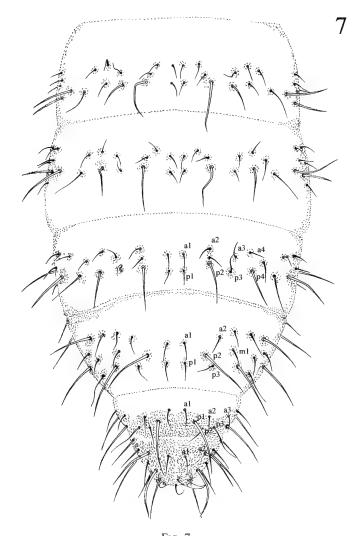


Fig. 7

Cetatophysella tupamara sp. nov., \$\gamma\$ holotype. Abdominal chaetotaxy in dorsal view.

ETYMOLOGY: The species is named after José Gabriel Condorcanqui Noguera (Tinta, Virreinato del Peru, 19-III-1738 - Cuzco, 18-IV-1781), mainly known as "Túpac Amaru II", leader of the major insurrection in Peru against Spanish colonists in the 18th Century.

TAXONOMIC REMARKS: Although more than 130 species are known in the genus *Ceratophysella*, very few exist in some regions as South America and China. Three species have been cited from South America and seven from China (Jiang *et al.*, 2011; Wu & Yin, 2007; Yue & Fu, 2000), among which *C. baichengensis* and *C. yinae* can be compared with the new species from Peru.

Character	tupamara	denticulata	baichengensis	yinae
length in mm	1.5	0.8-1.2	1.1	1.2
apical bulb on Ant. IV	trilobed	simple	bilobed	bilobed
sensilla on Ant. IV	7	7	8	4
seta m4 on Th. I	macroseta	microseta	microseta	macroseta
ocular setae C1 and C3	subequal	different	subequal	subequal
labral papillae	4	6	? .	? `
lateral tooth on unguis	small	big	big	small
abd. IV setae between	2+2	3+3	3+3	3+3
macrosetae				
thick setae on dens	0	0	4	0

TABLE 1. Comparison between *C. tupamara* sp. nov., *C. denticulata*, *C. baichengensis* and *C. yinae*.

Table 1 presents a comparison between those two Chinese species, the cospomolitan *C. denticulata* and *C. tupamara* sp. nov. The new species, besides being the biggest of all, has a trilobed apical bulb, which is simple in *C. denticulata* and bilobed in the two Chinese taxa. The ocular seta C1 and C3 are distinctly different only in *C. denticulata*. There are important differences in the chaetotaxy among *C. tupamara* sp. nov. and the other species: most of its macrosetae are barbulate; on Abd. IV there are only 2+2 setae between the macrosetae p2, while there are 3+3 in the other species. Only in the new species and in *C. yinae* are the setae m4 on Th. I macrosetae. Among these four taxa, *C. baichengensis* has four thick setae on the dens, which are normally developed in the other species.

Besides, *C. tupamara* sp. nov. and *C. denticulata* share the presence of seven sensilla dorsally on Ant. IV, while in *C. baichengensis* there are eight, and only four in *C. yinae*. *Ceratophysella tupamara* sp. nov. and *C. denticulata* have one macroseta P1 on Abd. V widely separate; *C. denticulata* has four setae between their bases, and the new species only two setae. *Ceratophysella baichengensis* has a smaller number of granules between setae p1 on Abd. V (8-10 versus 10-14 in *C. tupamara* sp. nov).

ACKNOWLEDGEMENTS

Dr Peter Schwendinger (MHNG) supported our study of South-American Collembola from the collection of the Muséum d'histoire naturelle de Genève. Blanca Mejía Recamier (Fac. Sciences, UNAM) made microscopic slides of the specimens, and Elihú Catalán assisted in the illustration of the new species.

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A new species of *Neoechinorhynchus* (Eoacanthocephala: Neoechinorhynchidae) from *Pachyurus bonariensis* (Perciformes: Sciaenidae) from the Paraná River basin in Argentina, with comments on two other species of the genus

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A new species of Neoechinorhynchus (Eoacanthocephala: Neoechinorhynchidae) from Pachyurus bonariensis (Perciformes: Sciaenidae) from the Paraná River basin in Argentina, with comments on two other **species of the genus. -** Neoechinorhynchus (Hebesoma) colastinense sp. n. is described from the intestine of Pachyurus bonariensis a freshwater fish from Paraná River basin. The new species is characterized by having a cylindrical trunk, elongated but swollen anteriorly; a spherical proboscis with a prominent apical organ; the anterior circle of hooks very large, alternating in 2 levels, separated from more posterior circles of hooks, but sometimes surpassing the hooks of the middle and posterior circles; a relatively long neck; the male reproductive system occupying 78-81% (79%) of the trunk length; the female reproductive system occupying 27-39% (32%) of the trunk length; and eggs elongated with polar prolongation of the fertilization membrane. Members of the species can be distinguished easily from the other species of South American Neoechinorhynchus Stiles & Hassall, 1905 because they are the only ones with characteristics of the subgenus *Hebesoma*. Additionally, two other species are recorded for the first time in Argentina: Neoechinorhynchus (Neoechinorhynchus) macronucleatus Machado Filho, 1954 from Lycengraulis grossidens and N. (N.) pimelodi Brasil-Sato & Pavanelli, 1998 from several species of *Pimelodus*. The presence of an apical organ at the proboscis tip is recorded in the new species and N. (N.) macronucleatus. Studies using scanning electron microscopy revealed the presence of non-rimmed pores in the tegument throughout the trunk, neck and proboscis of all three species. A key to the South American species of *Neoechinorhynchus* is provided.

Keywords: Taxonomy - morphology - Acanthocephala - *Neoechino - rhynchus - Hebesoma* - freshwater fishes - South America.

INTRODUCTION

Nine out of the more than ninety valid species of *Neoechinorhynchus* Stiles & Hassall, 1905 are known from South America (Amin, 2002; Amin & Heckman, 2009; Salgado-Maldonado *et al.*, 2010). To date, only one species of *Neoechinorhynchus* has been reported from Argentina, named *N. (N.) villoldoi* Vizcaíno, 1992 from *Corydoras paleatus* (Jenyns, 1842) (see Vizcaíno, 1992; Amin, 2002).

As part of a study on the Acanthocephala in Argentina, the examination of freshwater fishes collected in the Paraná River basin revealed the presence of a previously unknown species of *Neoechinorhynchus* and two known species that are recorded for the first time in Argentina. The objective of this study is to describe the new species and to give new data on other species based on recently collected material. Additionally, scanning electron microscopy micrographs, infection indices and comments on the spectrum of hosts of these species are provided.

MATERIAL AND METHODS

Fish were caught by local fishermen using hook and line and examined for parasites immediately after capture at the following localities: i) Colastiné River (tributary of the Paraná River) (-31.6696° -60.6078°), Santa Fe Province (Middle Paraná River basin) from 2000 to 2010 [2 *Pachyurus bonariensis* Steindachner, 1879, 80 *Pimelodus albicans* (Valenciennes, 1840), 14 *P. argenteus* Perugia, 1891 and 276 *P. maculatus* Lacépède, 1803]; ii) Paraná-Guazú River (tributary of the Paraná River) (-33.9086° -58.8822°), Entre Ríos Province (Low Paraná River basin) from 2003 to 2010 [26 *Lycengraulis grossidens* (Agassiz, 1829), 15 *P. albicans*, 3 *P. argenteus* and 27 *P. maculatus*].

The acanthocephalans found in the intestine were washed in saline solution, relaxed in cold distilled water for 12 h, fixed in 4% formaldehyde solution and stored in 70% ethanol. Entire worms were hydrated through a gradual ethanol series and cleared and mounted temporarily in Amman's lactophenol, which allows the rotation of the specimen examined. Other specimens were stained with Langeron's alcoholic chlorhydric carmine (Langeron, 1949), differentiated in acid ethanol, dehydrated through a gradual ethanol series, cleared in beechwood creosote and finally mounted in Canada balsam. Eggs laid spontaneously during relaxation of the worms were fixed in 4% formaldehyde solution and examined in distilled water for drawing.

One specimen of the new species from *P. bonariensis*, 1 specimen of *N. (N.) macronucleatus* from *L. grossidens* and 2 specimens of *N. (N.) pimelodi* from *P. maculatus* from Argentina preserved in 70% ethanol were prepared for scanning electron microscopy (SEM) as follows: post-fixed in 1% osmium tetroxide, dried with hexamethyldisilazane (Riedel-De Haën®), mounted on stubs with adhesive tape, sputter coated with gold in a Thermo VG Scientific Polaron SC 7630 and examined with a Philips XL 30 scanning electron microscope.

The type material of the new species was deposited in the Parasitological Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN-Pa) and in the Natural History Museum, Geneva, Switzerland (MHNG INVE), and voucher material of *N.* (*N.*) *macronucleatus* and *N.* (*N.*) *pimelodi* was deposited in MACN-Pa.

Measurements include the range followed by the mean and number of measurements (n) in parentheses. All measurements are in micrometers (μm) unless otherwise stated. Trunk length excludes neck, proboscis, and bursa. Illustrations were made with the aid of a camera lucida attached to a Zeiss Axioskop microscope equipped with differential interference contrast optics. Abbreviation: LWR, length to width ratio (sensu Monks *et al.*, 2011) and cn, common name. The classification and authorities of the fish follow FishBase (Froese & Pauly, 2012). Prevalence (P), mean intensity of infection (I), and mean abundance (A) were calculated according to Bush *et al.* (1997).

RESULTS

A new species of *Neoechinorhynchus* allocated to the subgenus *Hebesoma* is described herein. In addition, *Neoechinorhynchus* (*Neoechinorhynchus*) macronucleatus and N. (N.) pimelodi are recorded for the first time in the Paraná River basin. Comparative data from these species is given in Table 1.

Neoechinorhynchus (Hebesoma) colastinense n. sp. Figs 1-8, 10, 13, 16, 19

TYPE MATERIAL: Holotype MANC-Pa No. 517/1 (male); allotype MANC-Pa No. 517/2 (female) and paratypes, MANC-Pa No. 517/3 (4 females) and MHNG INVE 79181 (1 male and 2 females) from *Pachyurus bonariensis*; Colastiné River, Santa Fe Province, Argentina.

ETYMOLOGY: The species is named after the type locality and means "from Colastiné."

DESCRIPTION

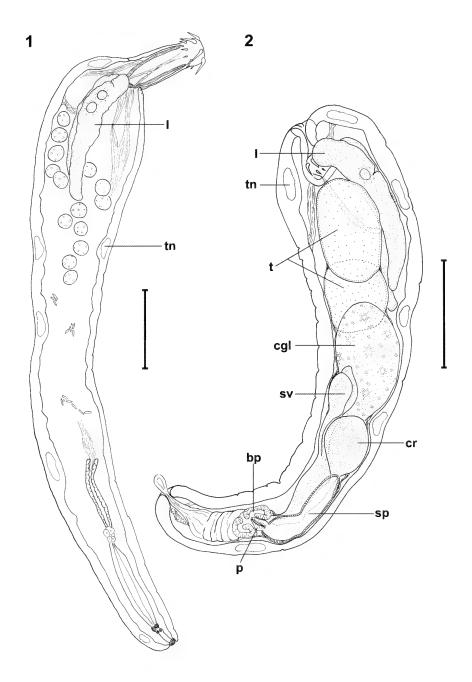
General (based on 10 specimens: 2 males, 7 gravid females and 1 juvenile female with ovarian balls used for SEM): Eoacanthocephala, Neoechinorhynchidae, with the characters of the genus Neoechinorhynchus and subgenus Hebesoma Van Cleave, 1928 (sensu Salgado-Maldonado, 1978; Amin, 2002). Fresh individuals white. Worms small. Trunk cylindrical, elongated, swollen anteriorly, curved ventrally, with 5 dorsal and one ventral giant nuclei, dorsal and ventral body wall similar in thickness (Figs 1, 2). Entire epidermal surface porous (Fig. 19). Sexual dimorphism usually inconspicuous. Proboscis spherical, wider than long (Fig. 3), with prominent apical organ (Fig. 10). Proboscis hooks in 3 circles of 6 hooks each. Hooks in anterior circle largest, alternating in two levels, separated from more posterior circles of hooks but sometimes surpassing the hooks of the middle and posterior circles, with simple roots directed posteriorly. Hooks of the middle and posterior circles much smaller than those of the anterior circle, with orbicular roots (Figs 3, 13). Neck relatively long, broader at base (Figs 1, 10, 16). Proboscis receptacle long, single-walled, extending for a short distance into the trunk when specimens are relaxed (Figs 1, 10); cerebral ganglion pyramidal-shaped situated near posterior end of receptacle (Figs 4, 10). Lemnisci subequal, digitiform, longer than proboscis receptacle, double-nucleated lemnisci usually slightly longer than single-nucleated lemnisci (Figs 1, 2, 4). Genital pore terminal in males and slightly subterminal in females (Figs 1, 2, 5).

Male: Trunk 2.6-3.2 mm (n = 2) long, 0.6-0.7 mm wide, LWR 5:1 (Fig. 2). Proboscis 90-110 (n = 2) long, 120-130 wide. Length of proboscis hooks in anterior

TABLE 1. Comparative records of hosts, localities and infection indices for three species of *Neoechinorhynchus* spp. found in Argentina and Brazil; data from Machado Filho (1954), Fabio (1983), Brasil-Sato & Pavanelli (1998, 1999), Santos & Brasil-Sato (2004) and present study.

,			,	*	,	
Parasite species	Host species	Locality	Site of infection	P (%)	Ι	A
Neoechinorhynchus (Hebesoma) colastinense n. sp.	Pachyurus bonariensis* (Perciformes: Sciaenidae) (cn: corvina de río)	Colastiné River, Santa Fe Province, Argentina**	middle intestine	50 (1/2)	10	0.5
Neoechinorhynchus (Neoechinorhynchus) macronucleatus	Lycengraulis sp.* (Clupeiformes: Engraulidae)	Juparaña lagoon, Espírito Santo State, Brazil**	intestine	I	1	1
	Hoplias malabaricus (Characiformes: Erythrinidae) (cn: tararira)	Municipio de Campos, Rio de Janeiro State, Brazil	intestine	2.2 (1/45)		0.02
	Lycengraulis grossidens (Clupeiformes: Engraulidae) (cn. anchoíta)	Paraná-Guazú River, Entre Ríos Province, Argentina	intestine	7.7 (2/26)	7.7 (2/26) 2.5 (2-3) 0.2	0.2
Neoechinorhynchys (Neoechinorhynchus) pimelodi	Pimelodus maculatus* (Siluriformes: Pimelodidae) (cn: bagre amarillo)	São Francisco River basin, Três Marias, Minas Gerais, Brazil**	anterior intestine	39.3 (94/239)	4.6	1.8
	Franciscodoras marmoratus (Siluriformes: Doradidae) (cn: bacu pedra)	Três Marias Dam, Minas intestine Gerais State, Brazil	intestine	10	4.3 (1-15) 0.4	0.4
	Pimelodus albicans (Siluriformes: Pimelodidae) (cn: bagre blanco)	Colastiné River, Santa Fe Province, Argentina	anterior intestine	2.5 (2/80) 6.5 (2-11) 0.2	6.5 (2-11)	0.2
	Pimelodus argenteus (Siluriformes: Pimelodidae) (cn: bagre)	Colastiné River, Santa Fe Province, Argentina	anterior intestine	7.1 (1/14)	2	0.1
	Pimelodus maculatus	Colastiné River, Santa Fe Province, Argentina	anterior intestine	2.9 (8/276)	4.4 (1-19)	0.1
*T** 50 50 5 ** ** ** ** ** ** ** ** ** ** ** ** *						

*Type host **Type locality



Figs 1-2

Neoechinorhynchus (Hebesoma) colastinense n. sp. from Pachyurus bonariensis. (1) Entire female worm, lateral view (allotype MACN-Pa 517/2). (2) Entire male worm with withdrawn proboscis, lateral view (holotype MACN-Pa 517/1). Abbreviations: bp = bursal pocket; cgl = cement gland; cr = cement reservoir; l = lemniscus; p = pennis; sp = Saeftigen pouch; sv = seminal vesicle; t = testes; tn = tegumental nuclei. Scale-bars 1-2 = 500 μ m.

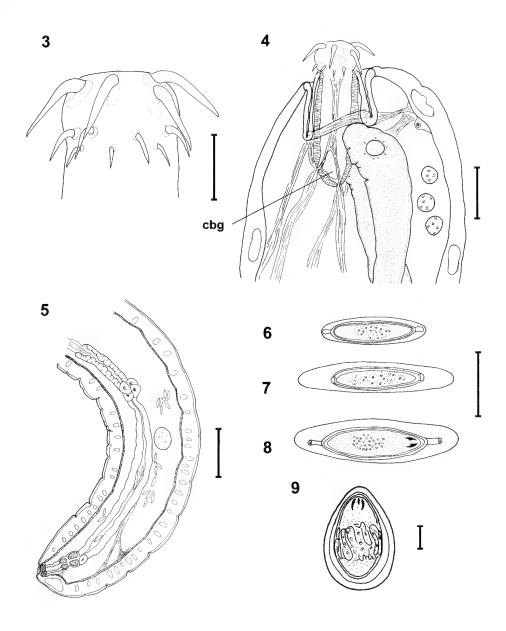
circle 80-95 (85; n = 4), in middle circle 40-45 (n = 2), in posterior circle 15-20 (n = 2); roots not measured. Apical organ 100 long (n = 1), 60 wide. Neck 285-300 (n = 2) long. Proboscis receptacle 350-360 (n = 2) long, 145-150 wide; cerebral ganglion 100-105 (n = 2) long, 35-70 wide. Lemnisci 815-1110 (975; n = 4) long, 150-200 (165) wide. Reproductive system approximately fills the trunk, testes overlap lemnisci, 2.1-2.5 mm (n = 2) in length, occupying 78-81% (79%) of total length. Testes oval, in tandem, overlapping, about equal in size but anterior testis slightly larger, 450-560 (n = 2) long, 300 wide, than posterior 365-530 (n = 2) long, 290-320 wide. Cement gland ovoid, about same size as testes, overlapping posterior testes, 480-535 (n = 2) long, 315-340 wide, with ovoid cement reservoir 280-300 (n = 2) long, 200-245 wide. Saefftigen's pouch 450-485 (n = 2) long, 120-165 wide. Penis 60-90 (n = 2) long, 30-50 wide. Bursa 420-460 (n = 2) long, 210 wide, with two bursal pockets (Fig. 2).

Female: Trunk 3.3-4.3 mm (3.9; n = 7) long, 0.6-0.8 mm (0.7) wide, LWR 5-6:1 (Fig. 1). Proboscis 115-140 (130; n = 4) long, 160-170 (165) wide. Length of proboscis hooks in anterior circle 100-115 (105; n = 7), in middle circle 40-55 (45; n = 7), in posterior circle 20-45 (35; n = 7); length of hook roots in anterior circle 50-60 (55; n = 6), in middle circle 10-20 (15; n = 6), in posterior circle 5-15 (10; n = 6). Apical organ 95-120 (105; n = 5) long, 55-85 (75) wide. Neck 36-475 (440; n = 3) long, 205-210 (n = 2) wide. Proboscis receptacle 435-475 (455; n = 7) long, 140-170 (155) wide;cerebral ganglion 95-150 (120; n = 7) long, 45-60 (55) wide. Lemnisci 775-1245 $(1065; n = 14) \log_{10} (145-190) = (175) \text{ wide (Figs 1, 4)}$. Reproductive system length 1.15-1.35 mm (1.25; n = 7), occupying 27-39% (32%) of total trunk length. Uterine bell 300-600 (435; n = 6) long, 50-100 (75) wide; uterus elongated 580-700 (660; n = 7)long, 80-115 (100) wide; vagina 160-200 (185; n = 7) long, 55-65 (60) wide (Figs 1, 5). Eggs elongated, outer membrane 40-65 (60; n = 10) long, 10-20 (15) wide; fertilization membrane with polar prolongations 40-55 (50; n = 10) long, 10-15 (11) wide; acanthor 30-40 (35; n = 10) long, 8-13 (9) wide; larval hooks 2-4 (3; n = 13) long (Figs 6-8).

DIFFERENTIAL DIAGNOSIS: The new species is characterized by the following combination of features: a cylindrical trunk, elongated and swollen anteriorly; a spherical proboscis with a prominent apical organ; an anterior circle of hooks very large, sometimes overlapping the middle and posterior circles of hooks; a relatively long neck; a male reproductive system occupying 78-81% (79%) of the total trunk length; a female reproductive system occupying 27%-39% (32%) of the trunk length; and elongated eggs with polar prolongations of fertilization membrane.

The eggs dispersed in the trunk cavity show different developmental stages of the polar prolongations of the fertilization membrane, from eggs without prolongations to eggs with prolongations not fully developed (Figs 6, 7). All the eggs measured in this description, which were those ripe and spontaneously laid during the fixation of adults, had such prolongations (Fig. 8).

Neoechinorhynchus (H.) colastinense sp. n. differs from all the South American neoechinorhynchids because it belongs to the subgenus Hebesoma (egg with polar prolongations of the fertilization membrane) (sensu Salgado-Maldonado, 1978; Amin, 2002), and by the large percentage of trunk cavity occupied by the female reproductive system (32%).



Figs 3-9

(3-8) Neoechinorhynchus (Hebesoma) colastinense sp. n. from Pachyurus bonariensis. (3) Armature of female proboscis (allotype MACN-Pa 517/2). (4) Detail of anterior region of trunk of the female worm, lateral view showing proboscis partially withdrawn and proboscis receptacle (paratype MACN-Pa 517/3). (5) Detail of female reproductive system, lateral view (paratype MACN-Pa 517/3). (6-8) Detail of eggs in different developmental stages of the polar prolongations of the fertilization membrane. (9) Neoechinorhynchus (Neoechinorhynchus) pimelodi from Pimelodus maculatus. Detail of drop-shaped egg. Abbreviations: cbg = cerebral ganglion. Scale-bars $3 = 100 \ \mu m$; $4-5 = 200 \ \mu m$; $6-8 = 25 \ \mu m$; $9 = 5 \ \mu m$.

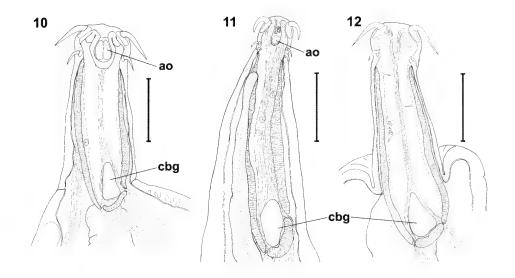
Only twelve of the more than ninety species of *Neoechinorhynchus* were placed on the subgenus Hebesoma, including species parasites of fishes and turtles from North America, Asia and India (Amin, 2002; Amin & Muzzall, 2009). Using Amin's key (see Amin, 2002), it is possible to discriminate the new species from the following North American species belonging to *Hebesoma* from fishes: N. (H.) agilis (Rudolphi, 1819) (with holarctic distribution), N. (H.) carinatus Buckner & Buckner, 1993, N. (H.) didelphis Amin, 2001, N. (H.) doryphorus Van Cleave & Bangham, 1949, N. (H.) idahoensis Amin & Heckmann, 1992, N. (H.) pungitius Dechtiar, 1971, and N. (H.) rostratus Amin & Bullock, 1998. Neoechinorhynchus (H.) colastinense sp. n. differs from N. (H.) agilis by having a shorter trunk length (2.6-4.3 versus up to 11.2) and the number of giant hypodermal nuclei (5 dorsal and one ventral versus 6 dorsal and two ventral); from N. (H.) carinatus and N. (H.) doryphorus by the length of the anterior circle of hooks (same length versus lateral anterior hooks longer than other hooks in the same circle); from N. (H.) didelphis by having a single uterine bell and the lack of neck girdle; from N. (H.) idahoensis by the length of hooks in anterior and middle circles (anterior circle of hooks much larger than the middle circle versus anterior and middle circles of similar length); from N. (H.) pungitius by having a larger proboscis in males and females (90-110 long, 120-130 wide and 115-140 long, 160-170 wide versus 57-90 long, 79-95 wide and 63-90 long, 84-118 wide), and the polar prolongations of fertilization membrane not extending to the outer shell; and from N. (H.) rostratus by having hooks rooted in all circles (versus only the anterior circle rooted). The new species differs from N. (H.) tenellus (Van Cleave, 1913), recently placed in Hebesoma (sensu Amin & Muzzall, 2009), mainly by having a longer neck (versus short), and a greater percentage of the trunk cavity occupied by the female reproductive system (32% versus 12%, respectively).

Neoechinorhynchus (Neoechinorhynchus) macronucleatus Machado Filho, 1954 Figs 11, 14, 17

MATERIAL STUDIED: MANC-Pa No. 518/1-2 (2 females) from *Lycengraulis grossidens*; Paraná-Guazú River, Entre Ríos Province, Argentina.

REMARKS: Machado Filho (1954) briefly described this species from the intestine of *Licengraulis* sp. from Brazil. Later, Fabio (1983) recorded one male specimen from *Hoplias malabaricus* (Bloch, 1794) also from Brazil. In Argentina, only five juvenile females were recovered from *L. grossidens*. The specimens are easily recognized because they have a cylindrical proboscis, the hooks of the anterior circle larger and stouter than the hooks in the middle and posterior circles, four prominent giant nuclei pre-equatorially situated in the dorsal body wall and lemnisci much longer than the proboscis receptacle.

In addition, minor differences were recorded in the measures of some characters while others were recorded for the first time: proboscis 110-135 (n = 2) long, 95-110 wide; length of hooks in anterior circle 40-50 (45; n = 4), in middle circle 25-35 (30; n = 4), in posterior circle 15-25 (20; n = 4); length of hook roots in anterior circle 40-50 (45; n = 4), in middle circle 5-15 (10; n = 3), in posterior circle 5 (n = 3); apical organ 65-75 (n = 2) long, 25 wide; proboscis receptacle 435-560 (n = 2) long, 110-125 wide; cerebral ganglion oval-shaped, situated near posterior end of receptacle 105-130



Figs 10-12

Neoechinorhynchus spp. females, details of anterior region of trunk. (10) Neoechinorhynchus (Hebesoma) colastinense sp. n. from Pachyurus bonariensis (allotype MACN-Pa 517/2). (11) N. (Neoechinorhynchus) macronucleatus from Lycengraulis grossidens (voucher MACN-Pa 518/1-2). (12) N. (N.) pimelodi from Pimelodus maculatus (voucher MACN-Pa 519/3). Abbreviations: ao = apical organ; cbg = cerebral ganglion. Scale-bars 10-12 = 200 μm.

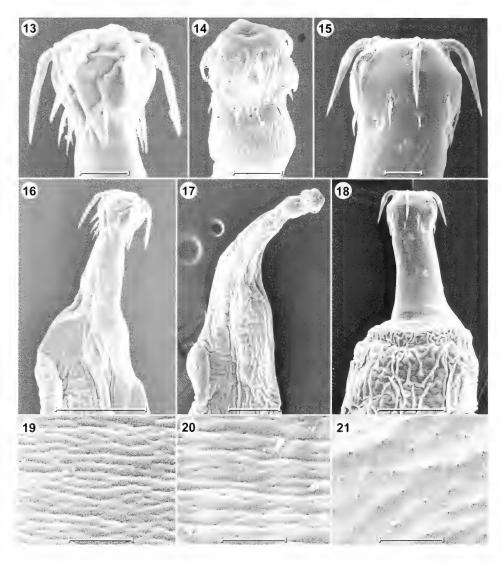
(n = 2) long, 50-65 wide (Figs 11, 14, 17). The presence of an apical organ, cerebral ganglion and roots of hooks in middle and posterior circle are recorded for the first time, and this is the first study of N. (N.) macronucleatus using SEM.

Neoechinorhynchus (Neoechinorhynchus) pimelodi Brasil-Sato & Pavanelli, 1998 Figs 9, 12, 15, 18, 20, 21

MATERIAL STUDIED: MANC-Pa No. 519/1 (3 males and 5 females) from *P. albicans;* MANC-Pa No. 519/2 (2 females) from *P. argenteus*; and MANC-Pa No. 519/3 (6 males and 7 females) from *P. maculatus*; Colastiné River, Sante Fe Province, Argentina.

REMARKS: This species was originally described by Brasil-Sato & Pavanelli (1998) from *Pimelodus maculatus* and later from *Franciscodoras marmoratus* (Lütken, 1874) (Siluriformes: Doradidae) by Santos & Brasil-Sato (2004), both from São Francisco River in Brazil. In Argentina, this species was found in the type host *P. maculatus* and also in two previously unrecorded hosts, *P. albicans* and *P. argenteus*; all of the hosts belong to the Pimelodidae. This is also the first record of this species from the Paraná River basin. The SEM studies on this species made by Brasil-Sato & Pavanelli (1998) showed only the copulatory bursa, but herein we include the proboscis, anterior trunk extremity, and the porous tegumental surface (Figs 15, 18, 20, 21).

The specimens from Argentina are larger than those from Brazil. Some of the differences recorded in males and females are, for example, length of trunk (2.8-6.3 mm and 2.2-6.8 mm, respectively), proboscis dimensions (115-175 long, 120-195 wide and 135-175 long, 130-200 wide, respectively), proboscis receptacle length (450-635



FIGS 13-21

Neoechinorhynchus spp. females, SEM micrographs. (13-15) Detail of proboscis. (13) N. (*Hebesoma*) colastinense sp. n. (14) N. (*Neoechinorhynchus*) macronucleatus. (15). N. (N.) pimelodi; (16-18). Anterior trunk and neck. (16) N. (N.) colastinense. (17) N. (N.) macronucleatus. (18) N. (N.) pimelodi. (19-21) Detail of porous tegument. (19) N. (N.) colastinense sp. n., anterior trunk. (20) N. (N.) pimelodi, anterior trunk. (21) N. (N.) pimelodi, posterior trunk. Scalebars 13-15 = 50 μm; 16-18 = 200 μm; 19-21 = 1 μm.

and 450-630, respectively) (Fig. 12), and lemnisci length (980-2500 and 1020-2220, respectively). Brasil-Sato & Pavanelli (1998) measured only the outer membrane of the eggs, now the size of each component of the eggs was determined: outer membrane 22-25 (24; n = 4) long, 15-17 (16) wide versus 15-22 (18) long, 12-15 (14) wide in the

Brazilian specimens; fertilization membrane 21-23 (22; n = 4) long, 13-15 (14) wide; acanthor 18-21 (19; n = 4) long, 10-12 (11) wide; larval hooks 2-4 (3; n = 5) long (Fig. 9). The eggs of the new material are slightly larger than those from Brazil. This difference could be because the eggs measured by Brasil-Sato & Pavanelli (1998) are not completely mature (intrauterine or free in trunk cavity) versus spontaneously laid eggs in this work. However, the similarities in the shape of the trunk (elliptic), the shape of the proboscis (spherical), the apparent absence of the apical organ, the distribution and size of the proboscis hooks, the percentage of the trunk occupied by the reproductive system and the position of the genital pore in males and females, and particularly in the morphology of the eggs (drop-shaped) allowed assigning the specimens from Argentina to Neoechinorhynchus (N.) pimelodi. Thus, size differences could be due to differential growth rates from different hosts (see Amin & Muzzall, 2009). The low indices of infection (prevalence, mean intensity and mean abundance) recorded in all the hosts collected in the Paraná River basin do not allow establishing which the principal host is. Brasil-Sato & Pavanelli (1999) studied the prevalence and mean intensity of infection of N. (N.) pimelodi from P. maculatus in the São Francisco River (Brazil) during the drought and flooding period; its prevalence is much higher than that in Colastiné River (42-51% and 30-34% versus 2.9% in the present paper), whereas the mean intensity of infection is very similar (4.8-4.9 and 3.5-4.9 versus 4.4 in the present paper).

DISCUSSION

Salgado-Maldonado (1978) proposed the synonymy of the genus *Neoechino-rhynchus* Stiles & Hassal, 1905 with *Hebesoma* Van Cleave, 1928. This synonymy was accepted by Amin (2002), who recognized *Hebesoma* as a subgenus of *Neoechino-rhynchus* based on the polar prolongations of the egg fertilisation membrane. Subsequently, most authors accepted the use of the subgenus as an additional feature for species characterization and discrimination (e.g. Amin *et al.*, 2003; Barger *et al.*, 2004; Barger & Nickol, 2004; Barger, 2004; 2005; Amin & Christinson, 2005; Mikhailova & Atrashkevich, 2008; Amin & Muzzall, 2009; Amin & Heckman, 2009; Martínez-Aquino *et al.*, 2009; Salgado-Maldonado *et al.*, 2010). In agreement with these authors, the new species is here allocated to the subgenus *Hebesoma*.

None of the nine species of *Neoechinorhynchus* described from South America, except the new one described herein, belongs to the subgenus *Hebesoma* (eggs with polar prolongations of the fertilization membrane). Considering the importance of the morphology of the eggs to discriminate between species belonging to the subgenus *Neoechinorhynchus* or *Hebesoma*, it will be interesting to study only completely ripe eggs (see Fig. 8, present paper) of the South American species that were originally described as without polar prolongations.

Neoechinorhynchus (Neoechinorhynchus) golvani was originally described from Mexico. Later, Brasil-Sato & Pavanelli (1998) mentioned the occurrence of this parasite from the Amazon River in Brazil and Amin (2002) also mentioned N. (N.) golvani as present in Mexico and Brazil. Curiously, Thatcher (2006) only mentioned its presence in Mexico, and Portes Santos et al. (2008) did not include this species in their exhaustive checklist about the acanthocephalans from Brazil. In view of the fact that

no specimens of this species are deposited in any collection in Brazil (Dr. Knoff, Curator of Instituto Oswaldo Cruz, and Dr. Magalhães Volunteer Curator of Instituto Nacional de Pesquisas da Amazônia, Brazil; pers. comm.) and that almost all records of *N.* (*N.*) *golvani* are from Central America (e.g. Martínez-Aquino *et al.*, 2009; Monks *et al.*, 2011; Salgado-Maldonado *et al.*, 2010), the occurrence of *N.* (*N.*) *golvani* in South America should be considered as an erroneous reference.

The presence of an apical organ at the proboscis tip was infrequently recorded among South American species of *Neoechinorhynchus*, only two of 9 species (*N*. (*N*.) *buttnerae* and *N*. (*N*.) *curemai*). In this work, two of the 3 species studied [*N*. (*H*.) *cola-stinense* and *N*. (*N*.) *macronucleatus*] have an apical organ.

Among South American species of *Neoechinorhynchus*, only *N. (N.) curemai* and *N. (N.) pimelodi* have been studied with SEM (Brasil-Sato & Pavanelli, 1998; Martins *et al.*, 2000). Amin & Heckmann (2009) reported the presence of non-rimmed pores throughout the trunk, neck and proboscis in the tegument of *N. (N.) buckneri* from the USA; a similar porous surface was observed in the three species studied herein.

During this study, *Neoechynorhynchus* (*H.*) colastinense and *N.* (*N.*) macronucleatus were found only parasitizing *P. bonariensis* and *L. grossidens*, respectively, whereas *N.* (*N.*) pimelodi was found widespread in *P. albicans*, *P. argenteus* and *P. maculatus* from Colastiné River. However, *Pomphorhynchus sphaericus* Gil de Pertierra, Spatz & Doma, 1996, a parasite of *P. albicans* and *P. maculatus* from La Plata River in Argentina (Gil de Pertierra *et al.*, 1996), has never been found in Colastiné River.

Key to the South American species of Neoechinorhynchus:

-	
1a.	Eggs with concentric membranes, without polar prolongations of the fertilization membrane; subgenus <i>Neoechinorhynchus</i> Stiles & Hassall, 1905
1b.	Eggs with polar prolongations of the fertilization membrane; subgenus <i>Hebesoma</i> Van Cleave, 1928
2a.	Trunk ovoid, elliptical or fusiform, swollen equatorially; proboscis without apical organ
2b.	Trunk elongated, swollen anteriorly; proboscis with or without apical organ
3a.	Lemnisci much longer than proboscis receptacle (twice or more); male reproductive system occupies about 50% of trunk
3b.	Lemnisci longer than proboscis receptacle; male reproductive system occupies more than 60% of trunk
4a.	Sexual dimorphisms present; neck twice longer than the proboscis; lemnisci subequal, overlapping anterior testes; eggs drop-shaped
4b.	N. (N.) pimelodi Brasil-Sato & Pavanelli, 1998 Sexual dimorphisms absent; neck short; lenmisci unequal, reaching level of testes, but not overlapping them; eggs elongate
5a.	Neck short; lemnisci slightly longer than proboscis receptacle; cement gland almost same size than testes N. (N.) paraguayensis Machado Filho, 1959

- 7b. Dorsal tegument with giant nuclei not clustered in pre-equatorial region 8

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Platyceps karelini (Brandt, 1838) from Iran to Pakistan and revalidation of Coluber chesneii Martin, 1838 (Reptilia: Squamata: Colubrinae)

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Platyceps karelini (Brandt, 1838) from Iran to Pakistan and revalidation of Coluber chesneii Martin, 1838 (Reptilia: Squamata: Colubrinae). - The distribution and intraspecific variation of Platyceps karelini are scrutinized in the present study. This species features characteristic morphological conditions allowing a distinction from sympatric Platyceps spp. as well as the geographically separated P. ventromaculatus (Gray, 1834). Hybrids between P. karelini and P. rhodorachis (Jan, 1863) are described. Coluber chesneii Martin, 1838 is revalidated for formerly unassigned racer populations from Southeast Turkey to West Iran (P. cf. ventromaculatus auct.). This taxon and Zamenis rogersi Anderson, 1893 from Northeast Africa to the Near East are revealed to be conspecific with P. karelini.

Keywords: *Platyceps karelini chesneii* comb. n. - *P. karelini rogersi* comb. n. - *P. mintonorum* - *P. rhodorachis* - *P. ventromaculatus* - morpho logy - distribution - systematics - taxonomy - hybrids.

INTRODUCTION

Coluber (Tyria) karelini Brandt, 1838 described from the eastern coast of the Caspian Sea is distributed across Turan and Iran to Pakistan. It belongs to *Platyceps* Blyth, 1860, a mainly Afrotropical and Saharo-Sindian genus revalidated by Inger & Clark (1943) for several nominal racer species including *Zamenis rhodorachis* Jan, 1863 and *Coluber ventromaculatus* Gray, 1834 (reputed type species). For a long time neglected by subsequent herpetologists, *Platyceps* Blyth in addition comprises a number of Afro-Saharan and eastern Mediterranean racers (Schätti & Utiger, 2001) as well as, for instance, *Coluber karelini mintonorum* Mertens, 1969 from Baluchistan

(Pakistan), actually a valid species (Schätti & Stutz, 2005), and *Platyceps* cf. *ventro-maculatus* sensu Schätti (2006) from Libya to Iran.

Khan (1997) examined Pakistani *Platyceps karelini* (Brandt) and gave diagnostic characters allowing its distinction from *P. rhodorachis* (Jan) and *P. ventromaculatus* (Gray). However, tremendous confusion still exists as to the systematics, geographic ranges, and character variation in these species and *P. mintonorum* (Mertens). The present study investigates the morphology of southern populations of *P. karelini* (Iran to Pakistan) as well as their distribution limits and distinctive character states vis-à-vis sympatric *Platyceps* spp.

MATERIAL AND METHODS

Seventy-nine Platyceps karelini from the whole distribution range (forty from area under consideration), three P. karelini x P. rhodorachis and three supposed or potential hybrid racers from Afghanistan, Iran, and Turkmenistan as well as ten Iranian Coluber chesneii Martin were examined (Appendices A-C). Two P. karelini collected in 2009-10 by one of the junior authors (ERP) and housed in the Qom Department of Environment were not accessible for study. The examined material is deposited in the American Museum of Natural History, New York (AMNH), The Natural History Museum (formerly British Museum [Natural History]), London (BMNH), California Academy of Sciences, San Francisco (CAS), Field Museum of Natural History, Chicago (FMNH), Farhang Torki Ecology and Herpetology Center for Research, Nurabad, Lorestan (FTHR), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), Muséum d'histoire naturelle, Genève (MHNG), Muséum national d'Histoire naturelle, Paris (MNHN), Staatliches Museum für Tierkunde, Dresden (MTKD), Naturhistorisches Museum, Basel (NHMB), Naturhistorisches Museum, Wien (NMW), Pakistan Museum of Natural History (PMNH), Razi University Zoological Museum, Kermanshah (RUZM, CP series), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt on Main (SMF), Staatliches Museum für Naturkunde, Stuttgart (SMNS), Tarbiat Moallem University, Sabzevar (TMUS), National Museum of Natural History [Smithsonian Institution, United States National Museum], Washington (USNM), Zoological Institute, Russian Academy of Sciences, Saint Petersburg (ZISP), and the Museum für Naturkunde der Humboldt-Universität (formerly Zoologisches Museum), Berlin (ZMB). Further acronyms used in the text are GNM (Georgian National Museum, Tbilissi, housing the collections of the former 'Caucasian Museum'), HUJ (Hebrew University Zoological Museum, Jerusalem), MSNM (Museo Civico di Storia Naturale, Milano), MMTT (Muze-ye Melli-ye Tarikh-e Tabii, Tehran [Teheran]), NHMG (Naturhistoriska Riksmuseet, Göteborg), QDE (Qom Department of Environment), SAM (collection of Sherman A. Minton, Jr.), SNMB (Department of Zoology, Slovakian National Museum, Bratislava), ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn), ZSI (Zoological Survey of India, Kolkata [Calcutta], storing the 'Indian Museum' [formerly Museum of the Asiatic Society of Bengal] herpetological collection), and ZSM (Zoologische Staatssammlung, München).

Morphological terms and head measurements are explained in Schätti (1988) and Schätti & McCarthy (2004). A slash separates right and left side counts of bilateral

head scales. Data in parentheses indicate uncommon conditions (single value) or the range for a given character. The frequency of the occurrence of a presubocular (i.e., the scale situated between the anterior subocular, loreal and supralabials, regardless of its size) is given as the percentage of the right and left side counts of all specimens combined. 'Total body scales' (or 'sum') encompass ventrals and subcaudals. The reduction pattern (sequence) of dorsal scale rows (dsr) along the trunk is expressed in terms of ventrals and as a percentage of their total number (%ven) based upon the average of the right and left side; 'low' or 'high' are used as an alternative for 'lateral' and 'paravertebral' dsr levels (or positions), respectively; 'mixed' means that low and high rows are involved in a specific bilateral reduction; in this context, 'median' is synonymous with the vertebral row (two in case of even number of dsr). The number of dorsal crossbands comprises all markings extending over both flanks; two unilateral blotches are counted as one complete cross-band. Maxillary teeth were examined on the right bone.

Scientific names of the taxa discussed in this paper are usually given in full only at their first appearance in the text and the Discussion. Specimens quoted in the synonym and chresonym section but not studied by us are in brackets. Variant spelling (e versus i or a) takes into account phonetic differences between languages, for instance in the case of Sistan-ve Baluchestan (Iran) and Baluchistan (Pakistan) Provinces and basically identical place names in different countries (e.g., Serakhs in Iran instead of Sarahs [Sarakhs], Turkmenistan). Furthermore, we made an effort to use official or at least locally prevalent designations as, for example, Ashgabat instead of Ashkhabad, Garagum instead of Karakum Desert and Khulm (Kholm) rather than Tashqorghan ("Tashkurgan").

'Southern' Platyceps karelini refers to populations from within the scope of this study, i.e., Iran, Afghanistan, and Pakistan; 'northern' are those from former Republics of the USSR. Central Uzbekistan goes as far south as the latitude of Bukhara (Buxoro) except for the eastern appendage (Tashkent area, Fergana Valley). 'Northeastern' is used for populations from Southeast Kazakhstan to Tadzhikistan (see Tb. 3). Coordinates, usually from http://www.geonames.org, and altitudes of localities are given under the cited material or in Appendix A, and at the appropriate place in the case of racer taxa other than P. karelini. The position of some collecting sites were traced with the map in Aitchison (1889: "Chinkilok", "Helmand" [River], "Kilki"), Zarudnyj's (1896, 1898) itinerary reports, or information in Gabriel (1935, 1938 [maps]: Arusan; "Gulu Cahak" or "Gulu Kahak" and "Tscha Sam", incl. altitudes), Clark et al. (1969: "Herat to Islam Qala", altitude), Mertens (1969: Darzi Chah), Adamec (1973: Kamran), and Clark (1990: west of Herat, altitude). Blanford's (1876) Kerman record (three specimens incl. BMNH 1874.11.25.10) is mapped at the capital of that province. The origin of BMNH 1886.9.21.101 obtained along the Helmand River (Arghandab Rod) by the Afghan Delimitation Commission (pres. Col. Swinhoe) is arbitrarily plotted near Chahar Burjak. CAS 120540 found 10 km west of Khulm (Tashqorghan) in North Afghanistan is from "455 m" above sea level fide Clark (1990) and about 570 m a.s.l. according to the register ("1850 ft. elevation"), in agreement with the approximate coordinates (ca. 36°42'N 67°36'E) of the indicated collecting site. In the case of USNM 240003, the file entry says that the specimen was taken "80 km" southeast of Esfahan at "7200 ft." (2'217 m), i.e., in the Kuh-e Lagarbeh

(2'016 m, peak) area with altitudes mostly between ca. 1'500-1'700 m; we pinpoint the origin of this specimen at 32°24'N 52°05'E in the vicinity of Rahmatabad (ca. 1'600 m). SMNS 2381 from "Baluchistan" (leg. Zdenek Vogel) was probably obtained in northern Sistan-ve Baluchestan. "Hoseinabad" (Latifi, 1991) is a frequent place name (Hoseynabad) between 32°09'-32°52'N and 59°03'-59°37'E in Khorasan-e Jonubi (South Khorasan) and is arbitrarily plotted at 32°25'N 59°20'E. In addition, former Khorasan (Iran) comprises Khorasan-e Razavi (Central) and Shomali (North) Provinces. The map (Fig. 5) includes an entry based on photographic record from the vicinity of Qal'eh-ye Shir Ahmad (36°07'N 57°51'E, Khorasan-e Razavi) and one collecting site in Turkmenistan immediately across the frontier with Iran (Tunijev et al., 1998, see footnote 8).

RESULTS

Platyceps karelini (Brandt, 1838) – Karelin's Racer

Coluber (Tyria) Karelini [sic] Brandt, 1838: col. [241] 243, "sur la côte orientale de la mer Caspienne" [ZISP 1695-1700] (origin clarified by Strauch, 1873; type locality possibly

in SW Kazakhstan; see Northern Populations).

Choristodon brachycephalus Severczov, 1873b: 72 [unnumb. Tb.], footnote 2, "okrestnosti Khodzhenta" (vicinity of Khujand, Tadzhikistan) [ZISP 3581] (new replacement name for Ch. sogdianus Severczov, 1873a; syn. Strauch, 1873; see Northern Populations: first smallprint, Hybrid Racers, footnote 4).

Zamenis Karelinii [sic]. - Strauch, 1873: 110 [272], Pl. III [ZISP 1696] (incl. "Persien" [ZISP

1701-02], see Northern Populations: first smallprint).

Z.[amenis] ventrimaculatus [sic] (Gray, 1834) [partim]. – Blanford, 1876: 414 (incl. "Karmán" [Kerman, Iran]; "Kila-i-Fath" [Qala-i Fateh, Qaleh-e Fath], "Zamrán" [Kamran], see Distribution, Systematics: first smallprints, Hybrid Racers incl. first smallprint, Fig. 8 and Tb. 4; Sclater, 1891).

Zamenis ventrimaculatus [sic] [var.] karelini comb. n. - Boettger, 1888: 928 (see Northern

Populations, Systematics, footnote 5).

Zamenis Karelini [sic]. - Wood-Mason, 1889: 8 ("Chin Ralak" ["Afghan Bound. Comm."], see Boulenger, 1889; Sclater, 1891).

Zamenis rhodorachis Jan, 1863. - Boulenger, 1889: 102 ("Gulran encampment, Badghis"

[Herat], see Hybrid Racers incl. Fig. 7A, Tb. 4 and footnote 7; Boulenger, 1893).

Zamenis karelinii [sic]. – Boulenger, 1889: 102 ("Chinkilok" [34°31'N 61°52'E, ca. 1'050 m a.s.l., ZSI 13107, Sclater, 1891], "Helmand" [River], "Kilki", "Tirphul" ["Between Tirphul and Kilki" fide Boulenger, 1893]: incl. BMNH 1886.9.21.102-103, see Hybrid Racers, Figs 2A and 6B, Tb. 4). – Boulenger, 1890: 326 ("Afghanistan" [incl. Kandahar]: BMNH 1882.3.20.2, see Morphology incl. second smallprint, Tb. 3).

Zamenis karelini. – Sclater, 1891: 28 (incl. Quetta [ZSI 11694]).

?Zamenis ladaccensis [sic] (Anderson, 1871) [partim]. - Sclater, 1891: 27 (incl. "Zamran" [Blanford, 1876: probably ZSI 4616], see Systematics, Hybrid Racers: first smallprints).

Zamenis karelinii [sic]. - Boulenger, 1893: [381, 383] 401 ("New Gulran", see Hybrid Racers; Boulenger, 1889: as rhodorachis).

Zamenis carelinii [sic]. - Werner, 1893: 92 (head scales).

Zamenis karelini. - Nikolskij, 1897: 335 ("Gjarmaz in Persia orientali" [sic] [ca. 34°00'N 59°50'E, ca. 850 m, ZISP 8748]). – Zarudnyj, 1897: 359 ("Germau [...] Khunik" Mountains [Garmab, "Zirkukh"]: NMW 25446.4) 1).

¹⁾ Anderson (1999) indicated the "Zirkukh Region", i.e., "Zirkukh", "terra Zirckuch" or "Terra Zirkuch" (Zarudnyj, 1896, 1897; Nikolskij, 1900, 1916), between 31°00'-34°01'N [sic] and 60°00'-60°30'E in eastern Iran. At least the village Shir Gug (or Shirkuk, 33°01'N 59°30'E) at ca. 2'100 m a.s.l. as well as two collecting sites of *Platyceps karelini* in that region ("Germau" [Garmab], Bamrud) reported by Zarudnyj (1897) and Nikolskij (1900) lie within a much more limited area of Northeast Khorasan-e Jonubi (South Khorasan).

Zamenis karelinii [sic]. - Alcock & Finn, 1897: 563 (Afghan-Baluch border area [Pakistan, unspecified]). – Nikolskij, 1900: 403 (Bamrud "in terra Zirckuch" [33°38'N 60°05'E, ca. 930 m], "Bendun in Seistano" ["Bendan", i.e., Bandan, 31°24'N 60°44'E, ca. 730 m], and "Persia orientalis" [ZISP 9289-92], see footnote 1). - Annandale, 1904: 209 (incl. "Perso-Baluch frontier") and 1906: 197 (incl. "Seistan", see Distribution: second smallprint; McMahon, 1906).

Zamenis karelini. - Wall, 1911: 1034 (Bostan [30°26'N 67°01'E, ca. 1'575 m], Gulistan [30°36'N 66°35'E, ca. 1'450 m], Mastung, Pishin, Quetta, Wali Khan [29°53'N 66°51'E (vic. Mastung Road), ca. 1'650 m]). – Nikolskij, 1916: 10 (Kundar [Kondor, 32°15'N 59°39'E, ca. 1'870 m, ZISP 9993]). – Wall, 1923: 618 (summary review, see Morphology: second smallprint). – Moricz, 1929: 33 ("Bendan" [Bandan, 34°18'N 57°22'E, ca. 850 m], "Pul-i-Khatum" [Pasgah-e Pol-e Khatun, 35°58'N 61°07'E, ca. 400 m], "Turbet-i-Khejdari" [Torbat-e Heydariyeh, 35°16'N 59°13'E, ca. 1'350 m]).

Z.[amenis] karelinii [sic]. – Werner, 1929: [65] 71 (review).

Coluber Karelini [sic]. - Werner, 1936: 198, 201 (Arusan [NE Esfahan, Dasht-e Kavir, 34°08'N 55°07'E, ca. 990 m, not in NMW], "Tscha Sam" [Chah-e Sam], "Gulu Kahak" ["Gulu Cahak", Gulu Chahak], vic. Neh [Nehbandan], "Tauran" [Turan, 35°36'N 56°44'E, ca. 1'360 m, not in NMW]: NMW 25446.3, 25446.5-6).

Coluber karelini. - Smith, 1943: 169 (review, type locality "S.W. Asia").

Coluber (Platyceps) karelini. – Guibé, 1957: 139 ("Dash Bouroun" [Dashli Borun], "Sarakhs" [Serakhs]: MHNH 1957.59-60, see Conclusions, footnote 3, Figs 2B and 9A).

Coluber karelini [partim]. - Leviton, 1959: 454 [462], Tb. IV ("Chah-i-Angir" [Chah-i Anjir]: CAS 84634-36, see Schätti & Stutz, 2005: footnote 1).

Coluber rhodorachis ladacensis (Anderson, 1871) [partim]. – Leviton & Anderson, 1961: 275 (same material as in Leviton, 1959).

Coluber karelinii [sic] [partim]. - Raï, 1965: [20, 21] 43 [75], map 9 ("Kerdahan" ["Iran"]: MNHN 8722, 1999.8160, see Distribution, Tbs 2-3).

Coluber karelini [partim]. - Minton, 1966: [47] 122 [172] ("Quetta Dist.": near Pishin [incl. SAM 931], 2 miles east of Hanna [Urak Valley]: AMNH 96219-20, see footnote 3).

Coluber karelini. - Král, 1969: 63, Tb. 1 (vic. Ag Chah [ca. 36°55'N 66°11'E, ca. 280 m, SNMB ("SNM") 54]).

Coluber k. karelini. - Mertens, 1969: [3, 10] 56 (Darzi Chah [Afghanistan]; Khuzdar, Quetta: SMF 62924, 62940, 64629).

"Coluber species" [cf. karelini]. - Clark et al., 1969: 312, Fig. 1 [map] (between Herat and "Islam Qala" [Islam Qaleh]: CAS 103785).

Coluber karelinii [sic]. – Leviton & Anderson, 1970: [173] 195 (key, distribution).

Coluber karelini. - Tuck, 1971: 61, map 21 ("Khurasan: 1 km. S. Esfideh" [Esfeden]: USNM 148631).

Coluber k. karelini. – Nilson & Andrén, 1981: 139, Abb. 9 (10 km N Mobarakiyeh [Dasht-e Kavir, ca. 35°09'N 51°47'E (vic. Askarabad), ca. 800 m, NHMG ("G.N.M.") Re. ex. 4422]).

Coluber k. karelini [partim]. – Khan, 1982: [225] 226 (see Distribution: second smallprint).

Coluber (Coluber) karelini [partim]. – Mahendra, 1984: [286] 287 (incl. Platyceps mintonorum [Mertens, 1969], see footnote 3).

Coluber karelini. – Khan & Ahmed, 1987: 368, Tb. IV (Mastung, see Morphology: second smallprint).

Coluber karelini [partim]. - Clark, 1990: 33, [unnumb.] Tb. ("10 Km.W Tashkurgan" [Tashqorghan, Khulm] and "45 Km.W Herat": ?CAS 120540, 120714, see Systematics,

Hybrid Racers, Fig. 7B, Tb. 4).

Coluber karelini [partim]. - Latifi, 1991: [67] 104, Pl. [Fig. 34, map] (NW Esfahan ["Central Province"]: Kashan [33°59'N 51°27'E, ca. 950 m]; Golestan ["Mazandaran"]: Aq Qal'eh [37°01'N 54°27'E, ca. 30 m], Gonbad-e Qabus [37°15'N 55°10'E, ca. 60 m]; Central Khorasan [Khorasan-e Razavi]: Kalateh Nader [37°04'N 56°45'E, ca. 990 m], "Ghoochan" [Quchan, 37°06'N 58°31'E, ca. 1'320 m], Mashhad [36°18'N 59°37'E, ca. 1'000 m], Neyshabur [36°13'N 58°48'E, ca. 1'200 m], Sabzevar [36°13'N 57°41'E, ca. 920 m]; South Khorasan [Khorasan-e Jonubi]: Birjand [32°52'N 59°13'E, ca. 1'500 m],

"Ghaen" [Qa'en (Qayen), 33°44'N 59°11'E, ca. 1'450 m], Hoseinabad [Hoseynabad, see Material and Methods], Sarbisheh [32°36'N 59°49'E, ca. 1'830 m]; Semnan: "Gharmsar" ["Central Province", Garmsar 35°20'N 52°13'E, ca. 1'100 m], Shahrud [Emamshahr, 36°26'N 54°57'E, ca. 1'380 m], Torud [35°27'N 55°01'E, ca. 839 m]; Sistan-ve Baluchestan: Zabol [31°02'N 61°30'E, ca. 480 m], Zahedan [29°30'N 60°52'E, ca. 1'350 m], see Morphology [dimensions], Distribution). – Khan, 1997: [52] 56 [58], Figs 1, 2A, 6 [map], Tbs 1-3 (incl. Chaman [30°55'N 66°28'E, ca. 1'335 m], "Punj Pai" [Panjpai, 29°55'N 66°30'E, ca. 1'485 m], ?"Zob" [Zhob, 31°20'N 69°27'E, ca. 1'415 m], see Morphology: smallprints, Distribution: second smallprint, Fig. 5).

Coluber karelini. - Tunijev et al., 1998: 78 (Khiveabad [Turkmenistan, 37°11'N 59°33'É, ca.

650 m], see Material and Methods).

Coluber karelini [partim]. - Khan, 1999: 276, 288 (habitat types, see Distribution: second smallprint). - Latifi, 2000: [136] 261, Pl. [Fig. 34, map] (incl. Kerman and Yazd Provinces, see Distribution).

P.[latyceps] karelini comb. n. – Schätti & Utiger, 2001: 935 (see Systematics: second smallprint). Coluber karelini [partim]. – Khan, 2002: [23, 30, 45 ("k. karelini", "k. mintonorum"), 57] 99, Figs 41-43 [coloured photographs of specimens from "Turkmenistan" (ca. 40 km east of Ashgabat along Garagum Canal) and "Iran" (26 km north of Gonabad, 34°38'N 58°46'E, ca. 900 m, MMTT specimen), resp.], 45a-c [head views, dorsal colour pattern], map 7 (see Distribution: second smallprint, Acknowledgements).

Coluber k. karelini. – Khan, 2004: 196 ("Pakistan" [checklist]); Firouz, 2005: 203 (provinces "10, 13, 14, 24, 25", fide Latifi, 1991 [1985], see Distribution).

Platyceps karelini. – Nagy et al., 2004: 224, 230, Figs 2-4 (mitochondrial [4] and nuclear [1] genes, see Systematics) and Lawson et al., 2005: 583, Figs 1-3 (DNA sequences [cyt b, c-mos]: CAS 184636 [SW Turkmenistan]). – Schätti et al., 2005: Abb. 8 (molecular data: 2443.03 [Uzbekistan: Bukhara (Buxoro)], see Systematics: second smallprint).

Platyceps cf. ventromaculatus [partim]. - Schätti, 2006: 677 (Dashli Borun: MNHN 1957.59,

see Systematics, Conclusions, Fig. 2B).

Coluber k. karelini [partim]. - Khan, 2006: [4, 17, 38 (Fig. 28.Biii)] 195, Tb. 10.1 [altitudinal distribution], map (see Morphology: third smallprint, Distribution: second smallprint).

Platyceps k. karelini. - Rastegar Pouyani et al., 2008: 18 ("Iran" [checklist, incl. "P. k. minto norum"]).

MORPHOLOGY

Head 2.0-2.47 times longer than broad. Rostral 1.40-1.80 times broader than high (see Hybrid Racers; second smallprint). Internasals and prefrontals about equal in size; the latter coalesced in a specimen from Arusan (Werner, 1936) of unknown whereabouts. Frontal 1.21-1.53 times longer than broad, 1.18-1.63 times longer than internasals and prefrontals, 0.92-1.22 times as long as parietals. Posterior border of the latter straight, slightly indented at the median suture, or forming an obtuse concave angle.

Nostril-eye distance 0.69-0.90 times length of internasals and prefrontals. Loreal usually as long as high, situated on third and posterior part of second supralabials; fused with nasal in AMNH 96220 (both sides) and TMUS 1002 (right); two superposed loreals in USNM 148631. Preocular entire and in contact with frontal except in BMNH 1882.3.20.2 (right side), FMNH 141604, and MNHN 1957.60. Anterior subocular always present; presubocular absent (59% based upon specimens with pertinent data, see Material and Methods) or present (41%, bilateral in BMNH 1882.3.20.2, 1886.9.21.102, CAS 103785, MNHN 1957.59, 1999.8160, NMW 25446.5, PMNH 761, RUZM 11.1, SMF 62924, 62940, USNM 148631 and 240003 [Fig. 10A] as well as on one side in MHNG 2718.12, MNHN 8722, and NMW

25446.4). Mertens's (1969) remark regarding the presence of an additional scale (presubocular) below the loreal in SMF 64629 ("als ein zweites (unteres) Loreale ausgebildet") is by mistake; there is no presubocular nor any other supplementary scale between the anterior subocular, loreal and supralabials.

Normally nine supralabials; eight on one side in the unregistered Qom specimen, AMNH 96220 with eight/ten, ten in CAS 103785 and on the ride side of BMNH 1882.3.20.2, CAS 84634, and PMNH 761. Fifth supralabial in contact with eye (unilaterally sixth in AMNH 96220 and PMNH 761); orbit completely separated from supralabials by a row of three suboculars (i.e., fifth supralabial horizontally divided) in TMUS 1002. Posterior subocular distinctly larger than anterior. Two postoculars and anterior temporals (see footnote 7); two or three scales in second temporal row; lower anterior scale larger (upper particularly small in, e.g., NMW 25446.6 and SMNS 2381 or on left side of SMF 64629, see also Fig. 4C).

Khan (1997) notified that "in 97%" (n=27) of Pakistani specimens the fifth supralabial enters the eye and "3% have 5th on one side and 5th and 6th on the other, one specimen has none in contact on one side, one on the other." However, the latter condition (supralabials unilaterally excluded from orbit) is not tabulated (l.c.: Tb. 1). Wall's (1911) remark that "the 3rd, 4th and 6th being divided, and the 4th, 5th and 6th touch the eye" is due to a different and incomprehensible terminology for supralabial scales. Leviton (1959) called the posterior subocular "subpost-ocular"; Minton (1966) and Mertens (1969) as well as many earlier authors (e.g., Strauch, 1873; Boettger, 1888) considered the anterior and posterior subocular scales as the lowest preocular and postocular, respectively.

Ten sublabials (nine in MNHN 1957.60), four in contact with first inframaxillary (three in USNM 148631), sixth largest. Anterior inframaxillaries shorter and broader than posterior pair (about the same length in MNHN 1957.59); posterior chin shields separated by two (occasionally three) rows of elongate or lanceolate scales anteriorly and four to five (three) behind. Gulars in four (three to five) oblique rows of scales between the caudal edge of the posterior inframaxillaries and the first ventral.

Strauch (1873: 116, 272) enumerated two specimens (ZISP 1701-02) of unknown gender from "Persien" (probably "Chorassan oder Kirman", coll. "Graf Keyserling") with 199-200 ventrals; the latter has 102 subcaudals (sum 302); "89" subcaudals for ZISP 1701 (sum 288) need confirmation (tail possibly incomplete). More ventrals ("2+216") and total body scales (320) than in Iranian females examined by us are reported from the Kavir Desert (NHMG 4422, Nilson & Andrén, 1981); these findings require verification. Data for BMNH 1882.3.20.2 (damaged &, 198 ventrals, 100 subcaudals) in Boulenger (1893: letter g, 193 and 98, respectively) are without missing ventrals. Wall (1911) notified as few as 192 ventrals (92-99 subcaudals) for "several specimens" (at least six, see chresonyms) deposited in the 'Quetta Museum'. In view of the proximity of these records to northern Kandahar (Tb. 3), we do not reject a priori this minimum (192); however, ventral counts of close to 190 in populations from Northeast Baluchistan Province are in need of confirmation. The report of up to 111 subcaudals by Wall (1923) is most probably from Central Asian *Platyceps karelini* as evidenced by the maximum (213) for ventrals

(see Northern Populations) ²⁾. The by far highest number of subcaudals (110) for Pakistan (Khan & Ahmed, 1987) in a specimen of unknown gender from Mastung remains unconsidered in this study. Khan's (1997) total body scale counts (282-317) are not based upon individual data but are simply the sum of the extremes for ventrals (192-207) and subcaudals (90-110). Brück's (1968) "karelinii" [sic] from the Morghab (Murgab) in Northwest Afghanistan with 147-150 ventrals, 62-90 subcaudals, and including a melanistic individual belong to a colubrid genus different from *Platyceps* Blyth (see next smallprint).

Dorsal scales with paired apical pits, normally in 19-19-13 rows along trunk (Tb. 1) ³⁾. Males with this formula have the first and second bilateral reductions between ventrals 114.5-128 (56-62%ven) and 117.5-129.5 (57-64%ven), respectively; the third (last) is situated at ventrals 138-165.5 (67-80%ven). The most cranial positions are from TMUS 994; whereas differences versus all remaining males with pertinent data are slight in the case of the anterior reductions, the third (at ventral 138 or 67%ven) is much farther cranial than the second lowest absolute level (146, AMNH 96219) or relative position (72%ven, MHNG 2718.11). All females conform to the standard formula (19-19-13 dsr). With the exception of MNHN 1957.60 (see footnote 3) and USNM 148631 (reduces to 17 dsr at ventral 110.5 or 53%ven and to 13 dsr at 140.5 or 68%), the verified reductions occur between ventrals 116.5 to over 125 in NMW 25446.5 (55-62%ven), 118.5-128.5 (57-63%ven), and 143-166.5 (69-80%ven), respectively.

More often than not, the first reduction is paravertebral followed by a lateral fusion (Tb. 1). Usually, rows 2-4 and 7-9 are involved in the anterior reductions; the sixth row participates unilaterally in MNHN 1957.60 and TMUS 1002 (17-15 dsr); the vertebral involves in AMNH 96220, SMNS 2381, and USNM 148631 (19-17 dsr). The transverse positions of the first and second reductions are mixed in MHNG 2718.12; another male (ZMB 6876) reduces to 17 dsr ('low-high') on the left side followed by the reversed sequence to 15 dsr on the right. The third reduction usually involves rows 6-8 (5-7 in AMNH 96219); the vertebral row participates in CAS 84636, 103785, 120714, FMNH 141604, MHNG 2718.12, NMW 25446.4, SMF 62924, SMNS 2381 as well as USNM 148631 and 240003 (SMNS 2381 and USNM 148631 with an additional median reduction farther cranial, see above).

The reductions of SMF 64629 (3) with 19-19-11 dsr involve rows 8+9, 3+4, 6+7, and 5+6 between 50-89%ven. Two males from near Kandahar (MNHN 8722, 1999.8160) show aberrant overall patterns (Tb. 2). In the former, the reduction to 17 dsr and a vertebral split (immediately followed by a median fusion) occur before midbody (46-48%ven). Without taking account of the addition above ventral 104 (simultaneous with a lateral reduction on the same side), MNHN 1999.8160 exhibits five changes in the number of dsr involving the vertebral row.

²⁾ The ventral counts of many specimens mentioned in literature probably include one or two preventrals.

TABLE 1. Number of ventrals and dorsal scale row (dsr) reduction pattern in Platyceps karelini from Iran to Pakistan with 19-19-13 dsr at the 15th ventral, midbody (msr), and five ventrals prior to the vent (see footnote 3). The longitudinal positions (ventrals) indicate means for bilateral reductions; no precise data for third fusion of dsr in MNHN 1957.60 (approximate position, transverse level not ascertained) and anterior reductions of NMW 25446.4-5 (verified level with 19 and 15 dsr in parentheses). Abbreviations: lat (lateral), par (paravertebral), p+v (paravertebral levels and vertebral row).

Accession number	Ventrals	Positions along trunk in absolute numbers	unk in %ven	Transverse levels or remark (dsr)	Gender and origin
AMNH 96219	198	115.5, 119, 146	58, 60, 74	par - lat - par	d. Pakistan
AMNH 96220	205	119, 126, ?	58, 61, ?	p+v - lat -?	♂, Pakistan
BMNH 1882.3.20.2	198			19-19-13 dsr	♂, Afghanistan
CAS 84635	204	1	ı	? - ? - 13 dsr	3. Afghanistan
CAS 84636	209	1		19 msr	♂. Afghanistan
MHNG 2718.11	205	123, 128.5, 147.5	60, 63, 72	par - lat - par	đ, Iran
MHNG 2718.12	208	127.5, 129.5, 165.5	61, 62, 80	mixed - p+v	♂, Iran
NMW 25446.6	$\frac{203}{203}$	121. 129. 152	60, 64, 75	par - lat - par	♂, Iran
PMNH 761	207	1		19-19-13 dsr	♂. Pakistan
PMNH 762	198	1	,	19-19-13 dsr	♂, Pakistan
SMF 62924	200	117, 119, 148.5	59, 60, 74	par - lat - p+v	♂, Pakistan
TMUS 994	205	114.5, 117.5, 138	56, 57, 67	par - lat - par	β , Iran
TMUS 1000	206	120, 128.5, 150.5	58, 62, 73	par - lat - par	♂, Iran
TMUS 1002	206	128, 128.5, 163	62, 62, 79	Îat - par - par	♂, Iran
ZMB 6876	202	121, 124, 150.5	60, 61, 75	(see text) - par	♂, Iran
NMW 25446.3	202	1		19 msr	juv., Iran
TMUS 1001	205	1	1	19 msr	juv., Iran
unregistered (vic. Qom)	204	1	1	19-19-13 dsr	?, Iran
BMNH 1886.9.21.102	208	117, 122.5, 153	56, 59, 74	par - lat - par	9, Afghanistan
BMNH 1886.9.21.103	208	117.5, 122, 152	56, 59, 73	par - lat - par	9, Afghanistan
CAS 84634	212	117.5, 124.5, 147.5	55, 59, 70	par - lat - p+v	9, Afghanistan
CAS 103785	207	116.5, 118.5, 143	56, 57, 69	par - lat - p+v	9, Afghanistan
CAS 120714	509	121, 125.5, 166	58, 60, 79	lat - par - p+v	♀, Afghanistan
FMNH 141604	202	124.5, 126, 152.5	62, 62, 75	lat - par - p+v	Q, Iran
MNHN 1957.59	201	121.5, 123, 160.5	60, 61, 80	lat - par - par	♀, Iran
MNHN 1957.60	203	115.5, 116 (ca. 135)	57, 57 (ca. 67)	lat - par - ?	♀, Iran
NMW 25446.4	209	(120-128) 161	(57-61) 77	3 - 5 - p+v	⊋, Iran
NMW 25446.5	208	(125-135) 166.5	(60-65) 80	? - ? - par	♀, Iran
RUZM 11.1	204	119, 122, 151	58, 60, 74	par - lat - par	♀, Iran
SMF 62940	204	123, 128.5, 154	60, 63, 75	par - lat - par	9, Pakistan
SMNS 2381	207	121, 123.5, 159.5	58, 60, 77	p+v - lat - p+v	♀, Iran
USNM 148631	208	110.5, 119, 140.5	53, 57, 68	p+v - lat - p+v	♀, Iran
USNM 240003	204	118, 126, 148.5	58, 62, 73	par - lat - p+v	♀, Iran
				•	Africa

of ing

TABLE 2. 1 Kandahar, median row	TABLE 2. Dorsal scale row (dsr) reduction pattern of <i>Platyceps karelini</i> MNHN 8722 (197 ventrals) and 1999.8160 (196) from the vicinity of Kandahar, Afghanistan. Right (upper line) and left longitudinal positions in absolute numbers of ventrals. Changes in the number of dsr involvin median rows in boldface. Abbreviations: v.red. (vertebral reduction, in case of even number of dsr), v.s. (vertebral split).	ion pattern of <i>Pl</i> e) and left longit v.red. (vertebral r	atyceps karelini udinal positions ii eduction, in case	MNHN 8722 n absolute nun of even numb	ow (dsr) reduction pattern of <i>Platyceps karelini</i> MNHN 8722 (197 ventrals) and 1999.8160 tight (upper line) and left longitudinal positions in absolute numbers of ventrals. Changes in the Abbreviations: v.red. (vertebral reduction, in case of even number of dsr), v.s. (vertebral split).	99.8160 (196) fro iges in the number al split).	n the vicinity of dsr involvii
MNHN 8722	722						
	7+8 (91)		2+3 (118)	6+7 (129)	3+4 (169)	4=4+5 (183)	
19	17 v.s. (94) 18	17	15	1	13	11	13
	(06) 6	(56) 6+8	2+3 (115)	6+7 (129)	3+4 (167)	4=4+5 (182)	
MNHN 1	MNHN 1999.8160						
				8+9 (103)	3+4 and 8=8+9 (104)	8=8+9 (105)	8+6 (108)
19	18	19	18	-	16 [17]	16	17
	3+4 (97)	3=3+4 (100)	8+9 (101)	3+4 (103)			6+7 (107)
cont. MNHN 1999.8160	Ζ						
				3+4 (162)			
15	14 v.red. (129) 13	12	13		1		
	7+8 (127)	3+4 (158)	4=4+5 (160) 4+5 (162)	4+5 (162)			



Fig. 1

Male *Platyceps karelini* from Hoseynabad-e Mish Mast (34°27'13"N 51°10'02"E, Esfahan Province), approximately 35 km southeast of Qom, Iran (QDE specimen, see Material and Methods).

Longest specimens approximately 700 mm snout-vent length (\Im , NMW 25446.6, tail incomplete) and about 670 + 212 mm (\Im , SMF 62940); Khan & Ahmed's (1987) 680 + 230 mm are from a specimen of unknown gender (see smallprint above). Latifi's (1991) "107 cm; tail, 25 cm" may rely upon a taxon different from Karelin's Racer (see Comparison). Smallest individuals 185 mm snout-vent length (CAS 84636, fide Leviton, 1959) and 200 + 65 mm (NMW 25446.3). Tail/body ratio 0.31-0.40 for males and females.

Dorsal head colour pattern usually absent but often with a fine line along interparietal suture (Figs 1-2, 9A). A dark slanted subocular blotch and a dark oblique streak from the angle of the mouth to the anterior lateral border of the parietals always present. Exterior edge of supraocular diffusely brown or blackish above the eye in

BMNH 1886.9.21.102 (Fig. 2A), MNHN 8722, 1957.60, SMNS 2381, and a ODE Platvceps karelini (Fig. 1, see last paragraph of Comparison section regarding peculiarities of dorsal head pattern in examined specimens from SW Esfahan, Markazi, and Oom). MNHN 1957.59 (Fig. 2B, see Guibé, 1959) displays conspicuous deep black markings on the pileus made up of 'eyebrow' flecks, a broad mid-parietal line with bilateral twirls, a hexagonal protrusion at the fronto-parietal border (with a short median line running to a slightly less distinct dark area of similar size on anterior edge of frontal), a half-moon mark behind the parietals, and these scales encroached upon laterally by the temporal streak (also observed in SMNS 2381). The latter extends across the parietal meeting its counterpart mid-dorsally in BMNH 1886.9.21.102, forming an obtuse angle (Fig. 2A). Some specimens (e.g., MNHN 8722, 1957.60) show a roundish, subelliptic or short elongate nape spot. The latter is prominent in MNHN 1957.59 (see above, Fig. 2B) and connected to the post-parietal fleck by a short bar; a unilateral transverse line runs towards a dark mark behind the posterior exterior border of the parietal. A veritable nuchal streak is present in CAS 120714 and NMW 25446.5 (faint) or a QDE male (Fig. 1) and SMNS 2381, which have it fused with the first right nape blotch; in BMNH 1886.9.21.102 the right and left portion of the anteriormost cross-band are bent cranially and converge into a striking mid-dorsal wedgeshaped extension (Fig. 2A).

Body above creamish, pale grey, tan or buff with 41-60 brownish to black crossbands. They are widest on neck, narrower than interspaces, and distinct along the whole trunk but fading away on tail. Specimens from Afghanistan and Iran as well as AMNH 96220, SMF 62924, and SMF 62940 (Pakistan) have 41 to 54 complete transverse blotches. More (58-60) are found in three Pakistani *Platyceps karelini* (AMNH 96219, PMNH 761-62). On the neck, and sometimes farther behind (e.g., NMW 25446.6), the cross-bands may extend to the venter but they normally do not reach beyond the flanks and alternate, at least posteriorly, with a ventrolateral series of dark spots or bars usually encroaching upon the lateral edges of the ventrals. Underside of neck and venter ivory, ochre, or yellowish, sometimes with a pale orange (e.g., CAS 103785), pinkish, or salmon hue (Fig. 1).

The minimum for the number of complete cross-bands (41) is from SMNS 2381 with a vague origin (see Material and Methods) and the maxima for Iran and Afghanistan rely upon CAS 120714 (see below) and SMF 62940 (53). An unexamined QDE specimen has about 52 (Fig. 1, see Comparison). About 42 are present in MNHN 1957.60 (Fig. 9A, see Northern Populations: second smallprint); NHMG 4422 from Tehran [Teheran] Province shows 43 (Nilson & Andrén, 1981). Afghan specimens with pertinent data available (no counts ascertained for CAS 84634-36) have 45-54 or more complete dorsal bands (see Material and Methods); the maximum based upon CAS 120714 (Herat area) requires detailed definition. A potential Platyceps karelini x P. rhodorachis (CAS 120540) from North Afghanistan (Khulm) with approximately 78 comparatively short transverse blotches fits the number of dorsal markings (68-88) observed in two Tadzhik specimens (MHNG 2442.98, MTKD 16095) collected within less than 100 km airline from Khulm (see Northern Populations, Hybrid Racers). A "Coluber karelini" without origin reproduced in Khan (1993: Fig. 13, 1997: Fig. 3, and 2006: Pl. 123) is not this species as evidenced by over 70 cross-bands and the neck pattern. Actually, this picture is manipulated; in reality, two entangled snakes are discernible and the almost completely visible specimen is a Platyceps sp. other than Karelin's Racer, i.e., the taxon revalidated in this paper (see Systematics, Comparison: first smallprint, Conclusions). The report of a melanistic karelini

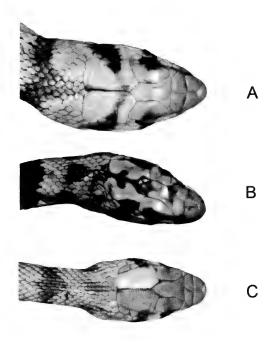


Fig. 2

Dorsal head pattern in *Platyceps karelini* from Afghanistan (A) and Iran (B-C): BMNH 1886.9.21.102 (A, Herat), MNHN 1957.59 (B, Golestan), and USNM 240003 (C, Esfahan, subadult, see Fig. 10A). Courtesy of Ivan Ineich/MNHN. Not to scale.

from "Afghanistan" (Brück, 1968, see smallprint above) is probably *Natrix tessellata* (Laurenti, 1768).

Maxillary with 13-15 or 16 (USNM 148631) teeth, anterior series subisodont, diastema usually wide, posterior two teeth enlarged, last offset laterad. Palatine with 8 (9), pterygoid 15-16 (Wall, 1911), and dentary (15) 16-19 teeth. Hemipenis subcylindrical, spinose at base, apical area calyculate; spines subequal in size except for the fringe of denticules along the sulcus spermaticus; border of calyces serrated (Fig. 3).

NORTHERN POPULATIONS

Platyceps karelini from Turkmenistan to Kyrgyzstan and Tadzhikistan (Appendix B) show mostly similar variation of head scales (see footnote 7), the number and reduction pattern of dorsal scale rows, body proportions, dentition (in particular maxillary and dentary teeth), and hemipenis ornamentation as observed in southern populations.

ZISP 19031.1 displays a loreal which is higher than long (Fig. 4C). The pre-ocular (entire in specimens from Iran to Afghanistan and Pakistan except CAS 120540: Fig. 7B, see Hybrid Racers) is divided in MTKD 13602 (right side), MTKD 16095 (both sides), and ZISP 19031.1 (right, with a faint cleft on the left); a short notch is dis-



Fig. 3

Sulcate view of everted left hemipenis of *Platyceps karelini* MHNG 2442.99. Scale equals 5 mm. Drawing Heidi Laubscher and Andrea Stutz.

cernible in ZISP 17219 (Figs 4C-D). A presubocular is absent in most *Platyceps karelini* from former Republics of the USSR; only SMF 18219, ZISP 17214.1, 19031.1, and ZMB 38816 show a bilateral scale of variable size in front of the anterior subocular (Figs 4B, 4D) ⁴⁾. ZISP 14741 (right) and 19031.1 (both sides) possess an additional (third) subocular completely excluding the eye from the supralabials (Figs 4A, 4D); this condition is also reported in two syntypes (Strauch, 1873: ZISP 1696, 1698). SMF 18220, ZISP 14741 (left), 17219, and 17682 (right) have ten supralabials (fifth or sixth in contact with eye); the same number occurs on both sides of ZISP 1706 (Strauch, 1873), an unlocated specimen from the lower course of the Murgab (Boettger, 1888: "10–10"), and on the right of an unspecified individual (Strauch, 1873: "als Duplicat

⁴⁾ A small granular scale between the anterior subocular ("Praeoculare inferius"), the loreal, and the third and fourth supralabials (Strauch, 1873) is observed in the holotype of *Choristodon brachycephalus* Severczov, 1873 (ZISP 3581) from Khujand ("Khodzhent" or "Chodshent", 40°17'N 69°38'E, ca. 320 m) in the Fergana Valley, Tadzhikistan. It has 200 ventrals, 85 subcaudals (Strauch, 1873, see Northern Populations: first smallprint), and the lowest total body scale count for *Platyceps karelini* reported in the literature consulted by us. This racer with about ("gegen") 80 short juxtaposed transverse dorsal bars is also noteworthy for the exceedingly developed cuneiform rostral wedged in deeply between the internasals ("Praefrontalia") and almost completely separating them, as well as the aberration of its head (right side shorter than left, hence the scientific species name) including an elliptic eye (Strauch, 1873). If not an otherwise aberrant specimen, ZISP 3581 is a malformed *P. karelini* x *P. rhodo-rachis* possibly descending from at least one crossbreed parent. The hybrid hypothesis is supported by comparative data for six *P. karelini* from Tadzhikistan (Appendix B) with 208-217 ventrals, 105-113 subcaudals (n=4), and a much higher sum thereof (315-323).

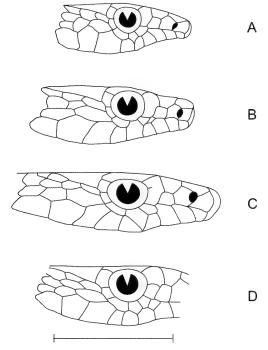


Fig. 4

Right lateral head scales of *Platyceps karelini* from Turkmenistan (B-D) and Uzbekistan (A, Karakalpakstan): ZISP 14741 (A), 17214.1 (B), 17219 (C), and 19031.1 (D). Variation of temporals as well as uncommon or rare conditions, i.e., shape of loreal (D), occurrence of a presubocular (B, D) or divided preocular (D), ten supralabials (C), and fifth supralabial excluded from contact with eye (A, D). Scale equals 10 mm. Drawings Heidi Laubscher and Andrea Stutz.

ausrangirt", see next smallprint) ⁵⁾. Eight supralabials are found in ZISP 17386 (right, fourth entering orbit) and 19031.1 (left). The upper portion of the right posterior subocular is split off in NMW 25446.1. The posterior subocular and the lower postocular are coalesced in ZISP 1697 (left) and 1698 (Strauch, 1873). Boettger (1888) noted a unilateral case of four scales along the posterior border of the eye ("Postocularen [...] 3–4") in a specimen from the Murgab Valley (see Morphology: first smallprint, footnote 5). ZISP 3647 has the left upper postocular fused with the supraocular plate (Strauch, 1873). We observed eleven (instead of the usual ten) sublabials on one side of MTKD 13436, NMW 25446.2, ZISP 17582 and 19031.2 as well as in ZMB 38816 ⁶⁾.

⁵⁾ We located and examined four out of six Turkmen *Platyceps karelini* reported by Boettger (1888), i.e., NMW 25446.1-2 (incl. possible hybrid) and SMF 18219-20. Two specimens of unknown gender obtained along the Murgab ("am Murgab") with 205-211 ventrals and 102-104 subcaudals, respectively, are possibly deposited in the "k. kaukasischen Museum" in Tbilissi (today incorporated into GNM collections) as notified in the introduction (l.c.: 875).

⁶⁾ Three out of five northern specimens with eleven sublabials (NMW 25446.2, ZISP 17582, ZMB 38816, see Hybrid Racers) originate from Southeast Turkmenistan. A higher than usual number of sublabials is also found in ZMB 38833 and on one side of BMNH 1873.1.7.10 (both *Platyceps karelini* x *P. rhodorachis*) as well as a potential hybrid from North Afghanistan (CAS 120540).

Ventrals 201-218 (\$\frac{\pi}{\pi}\$ 202-214, \$\Pi\$ 203-218, 201-217 in specimens of unknown gender), subcaudals 85-117 (88-117, 92-115, and 85-111, respectively), sum thereof 286-331 (293-331, 296-326, 286-323, resp., Tb. 3). Females of northern groups have slightly more ventrals than males. Northeastern populations (\$\frac{\pi}{\pi}\$, \$\Pi\$ \$\Pi\$) have higher means of ventrals and subcaudals than *Platyceps karelini* from any other area. Males from Southwest Kazakhstan to the Kopetdag (see footnote 8) and Bukhara (Buxoro, Uzbekistan) clearly differ from southern and eastern populations in the number of subcaudals (88-103 versus 102-117) and total body scales (293-310 vs. 308-331). Terentjev & Chernov (1940, 1949) and later authors notified 192-220 ventrals and 85-117 subcaudals (identical minima are quoted in, e.g., Bannikov *et al.*, 1977). Their lowest ventral count most probably relies on Wall's (1911, 1923) data for *P. karelini* from Pakistan (see Morphology: second smallprint).

ZISP 1705 and 3646-47 (Strauch, 1873) from "Kenderlinsk" (Kendirli Bay, SW Kazakhstan), "Karatschagly" in the Great Balkhan Range (NW Turkmenistan), and Uzbekistan ("Altes Bett des Oxus") are classified as females due to their high ventral counts (211-213, 97-100 subcaudals, Tb. 3). The minimum for subcaudals (85) also reported by, for instance, Boulenger (1890, 1893) is from two syntypes (Strauch, 1873: ZISP 1695-96, "Originalexemplar[e]"; type locality possibly in SW Kazakhstan) and the holotype of Choristodon brachycephalus Severczov from the Fergana Valley (see synonymy, Hybrid Racers, footnote 4). The latter (not allowed for in Tb. 3) accounts for the minimum (285) of ventrals and subcaudals combined in Strauch (1873: 273). Our lowest number (286) relies upon ZISP 1696; the tail of this possibly male syntype portrayed in Strauch (1873: Pl. III) appears to be intact. The morphological description of Platyceps karelini by this author encompasses data of twenty-one specimens including three that had been exchanged with other museums (the "Verzeichniss der [...] aufgestellten Exemplare" lists only eighteen deposited in the Imperial Academy of Sciences). This explains discrepancies between subcaudal counts (85-101 according to index versus up to 107 as indicated in the body of the text) and the maximum for ventrals ("bei fünf Stücken [...] mehr als 210"); to conclude from that latter remark, two out of three specimens then no longer in the St. Petersburg collections had more than 210 ventrals (Strauch, 1873: 113-14, 272-73). Boettger's (1888) "95" subcaudals for SMF 18220 from Durun is based upon an incomplete tail, and the lowest value ("91") in the Murgab series is considered incorrect (tip of tail most probably missing, see footnote 5). The maximum for ventrals (220) reported by Terentjev & Chernov (1940, 1949) may originate from one or several specimens collected in the northeastern portion of the distribution range; this count probably comprises one or two preventrals and the actual number may be identical with the maximum for ventrals (218, MHNG 2442.96) observed in this study (Tb. 3).

A female from Uzbekistan (ZISP 13110, see next smallprint) shows 17 midbody scale rows; the first reduction (19-17 dsr) occurs at ventral 71 (35%ven) by fusion of lateral rows. MTKD 16095 (3) with an irregular reduction formula has 17 dsr on a portion of the anterior trunk, 19 msr, and 11 dsr prior to the vent. A fourth fusion (13-11 dsr) involving paravertebral rows at ventral 166 (81%ven) is present in MHNG 1358.27 (3).

The verified number of dorsal cross-bands of most specimens from Turkmenistan (e.g., CAS 184636, MHNG 1358.27, MTKD 8281, NMW 25446.1-2, see Hybrid Racers: last paragraph) and MTKD 13602 from Southeast Kazakhstan (42 to ca. 55) is virtually identical to the range of *Platyceps karelini* from Iran and Afghanistan (41 to at least 54, see Morphology: third smallprint). Strauch (1873: incl. Pl. III) reported 40-48 in specimens from Southwest Kazakhstan, Turkmenistan, and ZISP 3647 from the original course of the Amu Darja (see smallprint above). However,

TABLE 3. Ventrals, subcaudals, and total body scales in *Platyceps karelini* from Iran to Central Asia and Baluchistan (Appendices A-B) including literature records. The Kandahar male sample comprises BMNH 1882.3.20.2, MNHN 8722, and MNHN 1999.8160 (see Tb. 2). Parentheses following the sample size (n) in the last column indicate number of specimens with intact tail. Boldface numbers denote literature data from Iran and Pakistan deemed in need of confirmation (see Morphology: second smallprint, Northern Populations incl. first smallprint, footnotes 2 and 4-5)

Gro	oup and region	Gender	Ventrals	Subcaudals	Total body scales	Literature source, remark
	SW Kazakhstan	88	$202-207$ (4) 204.5 ± 2.1	88-103 (4) 96.5 ± 6.6	293-310 (4) 301.0 ± 7.5	
	and N Turkmenistan to	unknown	201-209 (14) 205.1 ± 2.7	85-101 (12) 94.0 ± 5.3	286-306 (12) 298.9 ± 6.7	Strauch (1873), n=12 (11)
us	Central Uzbekistan	99	203-214 (13) 209.6 ± 3.8	92-106 (11) 97.3 ± 4.7	296-320 (11) 306.8 ± 8.5	Strauch (1873), n=3
latio		33	206-211 (5) 208.8 ± 2.2	$102-116 (5) 108.2 \pm 6.0$	308-326 (5) 317.0 ± 7.7	
ndod	SE Turkmenistan and S Uzbekistan	unknown	205-213 (4) 209.5 ± 3.4	102-110 (3) 105.3 ± 4.2	307-323(3) 315.0 ± 8.0	Boettger (1888), n=2
Northern populations		99	$204-216$ (2) 210.0 ± 8.5	106 (1)	310 (1)	
Nort	SE Kazakhstan Kyrgyzstan,	ð ð	207-214 (5) 210.2 ± 2.9	107-117 (4) 112.0 ± 4.2	314-331 (4) 321.8 ± 7.2	
	Tashkent area (E Uzbekistan), and	unknown	208-217(3) 211.7 ± 4.7	105-111 (2) 108.0 ± 4.2	315-319 (2) 317.0 ± 2.8	
	Tadzhikistan	99	211-218 (5) 214.1 ± 3.3	98-115 (4) 106.3 ± 7.7	316-326 (4) 320.5 ± 4.2	
		ð ð	202-208 (7) 204.9 ± 2.0	97-105 (5) 100.2 ± 3.3	303-310 (5) 304.8 ± 2.9	
Southern populations	Iran	unknown	199-205 (5) 202.0 ± 2.6	98-102(3) 100.0 ± 2.0	300-305(3) 302.3 ± 2.5	Strauch (1873), n=2 (1)
		φ φ	201-209 (9) 205.1 ± 2.9	92-106 (7) 98.6 ± 4.7	294-314 (7) 303.4 ± 6.4	
			216 (1)	104 (1)	320 (1)	Nilson & Andrén (1981)
	Afghanistan	3 3	204-209(3) 206.3 ± 2.5	105 (1)	311 (1)	
		0 0	196-198 (3) 197.0 ± 1.0	92-100 (3) 96.7 ± 4.2	288-298(3) 293.7 ± 5.1	Kandahar area
		φ φ	207-212 (5) 208.8 ± 1.9	91-105 (4) 101.3 ± 3.2	300-313 (4) 307.8 ± 6.0	
	Pakistan (NE Baluchistan)	33	198-207 (5) 201.6 ± 4.2	90-96 (4) 94.0 ± 2.7	290-303 (4) 296.5 ± 6.0	
		unknown	202 (1) 192 -206	- 92-99	-	Kahn & Ahmed (1987) Wall (1911), n≥6 (?)
		φ φ	204 (1)	97 (1)	301 (1)	

ZMB 38816 (\$) collected on the Turkmen-Khorasan border (Sarahs) has as much as about 65 transverse blotches, and even more (66-88) seem to be the rule in Kyrgyzstan and Tadzhikistan (MHNG 2442.96-98, MTKD 10450, 11335, 16095, NHMB 21058, ZMB 38591, see also Morphology: third smallprint, footnote 4). Two specimens from the vicinity of Bukhara (MHNG 2443.03, MTKD 13944) have at least 60 cross-bands.

In addition, ZMB 38816 differs vis-à-vis female *Platyceps karelini* from Southwest Kazakhstan, northern Turkmenistan and southeast to Tirmiz (Termez, ZISP 13110, 204 ventrals,

106 subcaudals) on the Uzbek-Afghan frontier (Balkh Province) in, for instance, a higher number of ventrals (216) as typically observed in females from Kyrgyzstan and Tadzhikistan (Tb. 3, see Hybrid Racers, footnote 7). MNHN 1957.60 (\$\partial Property, Fig. 9A) collected in the immediate vicinity (Serakhs, Khorasan-e Razavi) of ZMB 38816 across the Tedzhen (Harirud) River has 203 ventrals, 99 subcaudals, and as few as ca. 42 complete transverse dorsal markings (see Material and Methods, Morphology: third smallprint).

DISTRIBUTION

Platyceps karelini occurs from the northwestern Central Plateau (Iran) and the northeastern Caspian littoral (Kazakhstan) to the western Tien Shan region, the foothills of the Pamir, and Southwest Pakistan (Baluchistan). The northern limit of distribution is near 47°N latitude north of the former Aral Sea in Kazakhstan (Terentjev & Chernov, 1949: map 29; Bannikov et al., 1977: map 114). Brushko (1983) reports a specimen photographed between Mojyunkum (Furmanovka) and Mount Dzhambul, roughly 100 km airline from the southern end of Lake Balqash (Zhambyl Province, Kazakhstan). In the area under consideration, the species is known from east of the Zagros Mountains and the Atrek River (Golestan) in Iran to North Afghanistan (see below) and south through Yazd, Kerman, northern Sistan-ve Baluchestan (e.g., TMUS 1000; Annandale, 1906; Werner, 1936; Latifi, 1991; see next but one smallprint and Material and Methods regarding the origin of SMNS 2381), and western Afghanistan to Baluchistan (Fig. 5).

Mentions from the Arabian Peninsula (e.g., Anderson, 1896; Corkill & Cochrane, 1966; Gasperetti, 1974, 1977; Leviton, 1987; Leviton & Aldrich, 1984) rely on Bedriaga (1879) who erroneously assigned Blanford's (1876) *Zamenis ventrimaculatus* [sic] from Ras Musandam (Masandim) to Karelin's Racer (see Systematics). This specimen (ZMB 10324) from an insular promontory in northernmost Oman ("Cape Massandim, Arabian coast, entrance to Persian Gulf") belongs to *Platyceps* cf. *rhodorachis* (Jan), the only racer species living in that area.

Raï's (1965: map 9, p. 46) indication from Kermanshah in Northwest Iran is incorrect (see Comparison: second smallprint) and "Kerdahan" (MNHN 8722, 1999.8160) is Chahar Dahaneh near Kandahar, Afghanistan. Reports from Khuzestan and East Azarbayjan (Latifi, 2000) are based upon different Platyceps spp. The purported occurrence in "Markazi (Central Prov.)" notified by Firouz (2005: province no. 25) ultimately relies on Latifi's (1991) P. karelini from Kashan in Esfahan (see chresonyms). However, the westernmost verified collecting site (RUZM 11.1) is indeed from Markazi, i.e., about 20 km roughly southeast of Delijan close to the border with Esfahan. The species is also recorded from southeastern Tehran Province (NW Dasht-e Kavir, Nilson & Andrén, 1981) and adjacent Semnan (Garmsar, Latifi, 1991). Specimens from "Mazandaran" (Latifi, 1991, 2000) including ZMB 6876 were obtained in Golestan, which formed part of the former province until 1997. The reported presence all over Sistan-ve Baluchestan to as far south as the Gulf of Oman littoral (Latifi, 1991, 2000; maps) requires confirmation and, in particular, comparison with P. ventromaculatus (see Systematics). Information by local residents towards the senior author regarding the occurrence of P. karelini in Hormozgan is probably due to confusion with Lycodon striatus bicolor (Nikolskij, 1903) which shows a similar dorsal colour pattern. A recent herpetological investigation of that area by Rajabizadeh et al. (2008) did not provide any evidence for the presence of Karelin's Racer.

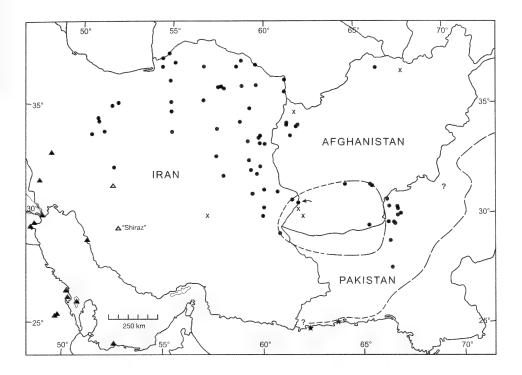


Fig. 5

Distribution records of Platyceps karelini (solid circles) in Afghanistan, Iran, and Pakistan including five entries (symbol X) based upon two P. karelini x P. rhodorachis from Afghanistan (Herat, Nimruz) and three supposed or potential hybrid racers from Iran (Kerman) and Afghanistan (Arghandab River, Nimruz and vic. Khulm, Balkh). The arrow in Southwest Afghanistan points to Kamran (see Systematics: first smallprint). The question mark in Northeast Baluchistan Province (Pakistan) accentuates reports from near Zhob (Khan, 1997). Triangles show collecting sites of examined Iranian Coluber chesneii Martin except MNHG 1359.12 (extralimital) and published records from Bahrain (various localities), Iraq (Faw Peninsula), Kuwait, Saudi Arabia, and Sir Bani Yas Island, UAE (see Schätti, 2006: 677-78, footnote 2); open symbols denote two intergrades from Fars, Iran (see Conclusions, footnote 10). The encircled area in the Baluchistan Region delimits the assumed distribution range of P. mintonorum (Latifi, 1991; Schätti & Stutz, 2005). The stippled line along the Indus Valley and the Makran coast indicates the approximate western distribution limit of P. ventromaculatus (Schätti & Schmitz, 2006: Fig. 3); two specified collecting sites (stars) in the Baluch littoral are Gwadar (25°07'N 62°20'E, BMNH 80.11.10.201) and Rumra (25°23'N 63°44'E, ZSM 222.1989, hoc loco). See text including Material and Methods, Hybrid Racers, and Appendices (A, C) for further explanations. Drawing Andrea Stutz.

In Afghanistan, *Platyceps karelini* is documented from Balkh (relies upon potential hybrid), Helmand, Herat, Jowzjan (Ag Chah), Kandahar, and Nimruz (see Systematics, Hybrid Racers: first smallprints). The species certainly occurs in Farah and two northwestern frontier provinces (Badghis, Faryab), may be found in parts of Ghor and Sar-e Pol (NW Afghanistan), and probably extends as far east as Kunduz. Boulenger's (1889) "Badghis" record based upon BMNH 1886.9.21.104 is from Herat (see Hybrid Racers).

Reliable Pakistani records are largely confined to Kalat, Khuzdar, Mastung (incl. Wali Khan), Pishin (incl. Bostan), Qila Abdullah (Chaman, Gulistan), and Quetta Districts in Northeast Baluchistan. Khan's (1997) mentions from "Zob" ("Loi Banda" and "Muslim Bazar"), i.e., Zhob (Fort Sandeman, 31°20'N 69°27'E), are in need of confirmation (Fig. 5). Mertens (1969) indicated *Platyceps karelini* from Northwest and Central Pakistan ("aus dem nordwestlichen bzw. mittleren Teile W-Pakistans") but his specimens only corroborate the presence at Darzi Chah in Afghanistan (SE Kandahar, "40 mi WNW Nushki", SMF 64629) close to the border with Pakistan as well as around Quetta and Khuzdar, the southeasternmost record of Karelin's Racer. The species certainly lives in the Nushki area as evidenced by SMF 64629. Sturdy or trustworthy reports, and in particular precise collecting sites, are lacking for Northwest Baluchistan Province, i.e., Chagai and northern Kharan where Karelin's Racer most probably occurs.

Parts of Chagai District were explored by, for example, the Afghan Delimitation Commission (Aitchison, 1889: map 1) and Alcock & Finn (1897). Annandale's (1904, 1906) determinations of ZSI specimens from unspecified localities in the border triangle of Afghanistan, Iran and Pakistan (Northwest Baluchistan) rely on Alcock & Finn (1897) and Arthur Henry McMahon. The inclusion of "Coluber karelini" among reptile species typical of "The Northwest Upland" (i.e., "from the high plains around Kalat and Quetta northeastward through Waziristan into the lower valleys of Swat, Dir, and Chitral") by Minton (1966: 40, map 5) is misleading; Platyceps karelini is not recorded from beyond Northeast Baluchistan Province. Khan's (1977) "karalini" [sic] from Darapathar near Rabwah (31°45'N 72°55'E, ca. 170 m a.s.l.), referred to as "an aberrent [sic] race" of "[t]he nominated [sic] taxon" from "arid Punjab" (Khan, 1982), is P. rhodorachis (see Comparison). Seven localities ("Boostan", Chaman, "Punj Pai", "Peshin", Quetta, and in the "Zob" area, see paragraph above) listed by Khan (1997: Appendix I; see also Wall, 1911; Minton, 1966) result in two or possibly three map entries on Pakistani territory along the frontier with Afghanistan; collecting sites as, for instance, Gulistan or Mastung (Wall, 1911; Khan & Ahmed, 1987) are not plotted. Khan (1999: 276, 288) regarded karelini to be a "widely distributed [mountain] species" also enumerated among the "large number of endemics" of the "Chagai-Kharan desert" ("Herpetologically riches [sic] part of Pakistan"). Khan (2002) reported P. karelini (as Coluber auct.) only "from Quetta and Pishin area" but three out of four entries on his map lie west of ca. 66°30'E longitude including the vicinity of Nushki (ca. 29°33'N 66°01'E, roughly 1'000 m) and Dalbandin (28°54'N 64°25'E, ca. 850 m), and thus are likely to refer to P. mintonorum (see Khan, 2002: 45). Not a single record from east or roughly north of Nushki is shown in Khan (2006: map) where merely three unspecified places are pinpointed; the southernmost and inexplicit locality mapped in Khan (2002) is missing, and the two western collecting sites most probably refer to P. mintonorum from Dalbandin and Nok Kundi (28°50'N 62°45°E, ca. 680 m) in Chagai (Schätti & Stutz, 2005: Fig. 1). According to Khan (2002: 99), P. karelini (type locality "Southwest Asia", possibly fide Smith, 1943), called the 'Banded desert racer' or 'spotted racer', "frequents plain deserts between 1500-3000 m of elevation in northwestern [sic] Balochistan"; earlier, the same species was denoted as the 'transversely striped desert racer' (Khan & Ahmed, 1987). It is further declared that "[s]pecimens have also been collected from northwestern [sic] Punjab, from Sulaiman Range" (Khan, 2006); a virtually identical remark ("I collected two specimens from the Sulaiman Range [...] in a rocky area") is hawked under "Coluber karelini mintonorum" and the putative origin left no mark on the accompanying map (see also Schätti, 2006: 683, 685; Schätti & Schmitz, 2006: smallprint p. 761). The occurrence of Karelin's Racer above 3'000 m as indicated by Khan (2006: Tb. 10.1) is unsubstantiated.

The confirmed altitudinal distribution on the Iranian Central Plateau ranges from approximately 700 m above sea level east of the Tahi Plain (TMUS 1001) in extreme eastern Yazd (Khorasan-e Jonubi border area) to about 1'870 m near Kondor in adjacent South Khorasan (Nikolskij, 1916; see Material and Methods as to USNM

240003). Similar altitudes (ca. 800 to at least 1'700 m) are attained on the northwestern Plateau. Lower elevations are inhabited around Zabol (ca. 480 m), along the Harirud (Tedzhen) River (Pasgah-e Pol-e Khatun, ca. 400 m; Serakhs, 280 m), and in Golestan where *Platyceps karelini* lives near sea level, for instance at Aq Qal'eh (Latifi, 1991). Afghan records are from ca. 280 m in Jowzjan (Ag Chah) to at least 1'000 m in the west and south (e.g., "Chinkilok" [Herat] or the vicinity of Kandahar including Chahar Dahaneh). To conclude from collecting sites in the immediate border area (Qila Abdullah District, Pakistan), the species most probably occurs at elevations of at least 1'200 m in Kandahar Province and elsewhere in Afghanistan. Three Pakistani specimens (AMNH 96219-20, SAM 931) were obtained close to 2'000 m "in a cultivated section of Urak Valley" (vic. Hanna, Quetta) and at ca. 1'530 m "in similar terrain near Pishin" (Minton, 1966). Altitudes nearing 2'000 m are inhabited around Kalat (PMNH 761). *P. karelini* from Quetta, Mastung, and Khuzdar (see Appendix A) were collected between ca. 1'200-1'700 m.

DISCUSSION

SYSTEMATICS

It is hardly an exaggeration to assert that *Platyceps* spp. from the western Sahara and eastern Mediterranean Region to the Himalayas (NW India) represented a taxonomic and systematic disarray for quite a long time. In particular, species from the eastern Caspian area to Pakistan still constitute a difficult problem to solve, confusing generations of zoologists since the days of Günther (1858).

Blanford (1876) synonymized Karelin's Racer, Zamenis rhodorachis Jan, 1863 and other taxa as, for instance, Coluber chesneii Martin, 1838 (type locality "Euphrates") with Coluber ventromaculatus Gray, 1834. With this relegation, Chesney's Racer vanished into the taxonomic muddle of the Platyceps rhodorachisventromaculatus complex for 130 years or so to come. Contemporary colleagues (e.g., Boettger, 1880; Murray, 1884) followed Blanford's (1876) view and thought Zamenis ventrimaculatus [sic] to be distributed from Egypt and the Arabian Peninsula to east of the Caspian Sea and Bengal. Boettger (1888) considered Coluber (Tyria) karelini Brandt, 1838 a colour variety ("Farbenvarietät") and ranked Karelin's Racer as a subspecies ("var.") of Z. ventrimaculatus [sic] auct. Boulenger (1890) re-established specific status for karelinii [sic], rhodorachis (as Z. ladacensis Anderson, 1871), and ventrimaculatus [sic]. Probably the best systematic herpetologist ever, in his monumental 'Catalogue', even Boulenger (1893) simply seemed to be overwhelmed when it came to the predicament of rhodorachis or ventromaculatus auct., and karelini as well (see Hybrid Racers incl. first smallprint).

Blanford's (1876) sample of *Zamenis ventrimaculatus* [sic] (see Distribution, Hybrid Racers: first smallprints) may not include any genuine *Platyceps karelini*. His series of twelve racers assigned to this confusing taxon comprises two specimens (no. "2, 3") obtained at Kamran ("Zamrán", 30°53'N 61°47'E, ca. 560 m above sea level) in Nimruz, Southwest Afghanistan, along the border with Iran (Fig. 5: arrow). Just one of them, ZSI 4616 or 8603 (Sclater, 1891: as *Z. ladaccensis* [sic], i.e., *P. rhodorachis*), has "the sixth supralabial [...] divided, so that there are three postoculars, and only the fifth supralabial enters the orbit." Its identity is unknown but the specimen undoubtedly may belong to *P. karelini* (Schätti & Schmitz, 2006: 761); however, the origin and the presence of a posterior subocular do clearly not exclude *P. mintonorum* (see

Comparison). The second Kamran "ventrimaculatus", apparently with two supralabials in contact with the eye, belongs to a *Platyceps* sp. other than *P. karelini* (see Hybrid Racers as to BMNH 1873.1.7.10 and 1886.9.21.101 from Nimruz).

Many field (and other) herpetologists remained perplexed regarding the diversity of morphological features of *Platyceps* spp. belonging to the *karelini-rhodorachis*ventromaculatus complex within geographically limited areas. To cite a more recent comment ("a complicated genus in S.W. and Central Asia"), we remind the reader that Clark's (1990) sample of eight "Coluber karelini Brandt" including the living one seen in "the Kabul bazaar" consists of three different species (P. karelini, P. mintonorum, P. rhodorachis) and a potential hybrid racer (see next chapter). Earlier, Leviton (1959) had "pointed out that [...] C. karelini, C. rhodorachis, and C. ventromaculatus, are known from southwestern Asia where their distributions overlap most extensively. They exhibit the same ranges of morphological variation, the same color pattern variations, and are found in similar environmental situations." Until recently, C. ventromaculatus auct., for instance, was by and large considered to be distributed from the Near East to northern India (e.g., Minton, 1966; Leviton et al., 1992; Khan, 1997; Disi et al., 2001: 267). In reality, P. ventromaculatus is only known from the lower parts of Northwest India and Pakistan where it extends along the Makran coast (Fig. 5) to at least as far west as Gwadar (Schätti & Schmitz, 2006: Fig. 3, footnote 2). A specific search would probably provide evidence for the presence of Gray's Racer in the littoral of Southeast Iran (Sistan-ve Baluchestan).

Platyceps cf. ventromaculatus sensu Schätti (2006), with Coluber chesneii Martin as its oldest available name, is a distinct taxon found from the eastern Mediterranean to at least as far east as Fars in Iran (Fig. 5, see Comparison). Chesney's Racer differs from *P. ventromaculatus* sensu stricto in, for instance, hemipenis features or molecular data (Schätti *et al.*, 2005: Abb. 8; Schätti, 2006) and is herewith revalidated. The systematic allocation of *C. chesneii* M. is addressed in the last chapter of this study (Conclusions).

Nagy et al. (2004) sequenced five nucleotides of seven nominal Platyceps spp. including "P. rogersi" (Anderson) from the Sinai, P. karelini (SW Turkmenistan), and P. rhodorachis (vic. Ashgabat). They found that the latter is "[b]asally linked to this six-taxon clade" and asserted that their "findings are of a strongly supported sister taxon relationship between P. karelini and the Arabian P. rogersi, thus excluding P. rhodorachis." However, there does not seem to be a reproductive barrier separating karelini and rhodorachis sensu stricto as substantiated by hybrids.

Schätti (2006: 675 [abstr.], 684) regarded Zamenis rogersi Anderson, 1893 to be conspecific with Platyceps cf. ventromaculatus. The senior author ranked Rogers's Racer as a junior synonym of this nomen operandum for unassigned Platyceps populations found in "comparatively mesic areas from northeast Africa to the Middle East" (Schätti & Schmitz, 2006) and suggested Coluber chesneii Martin as the correct scientific name ("may be a valid northern Saharo-Arabian taxon", see Conclusions). Based on nucleotide sequences (COI, 12S rDNA), P. cf. ventromaculatus is more closely related to P. cf. rhodorachis from Yemen than to P. ventromaculatus sensu stricto (Schätti et al., 2005: Abb. 8); incomplete data for P. karelini (only 12S partition) produced a sister taxon relationship with Chesney's Racer (cf. ventromaculatus) and cf. rhodorachis. In an earlier analysis without karelini, P. rogersi auct. appeared to be closely related to Yemeni cf. rhodorachis (Schätti & Utiger, 2001: Figs 8-9). Amr & Disi (2011) credited the latter authors with the inaccurate quote "that P. rogersi is well differentiated from P. ventromaculatus, while similar to the North African P. karelini [sic]. Their findings strongly supported

sister taxon relationship between *P. karelini* and the Arabian *P. rogersi*, thus excluding *P. rhodo-rachis* from the clade." The second assertion is incorrectly ascribed and has to be imputed to Nagy *et al.* (2004, see above).

HYBRID RACERS

Bogdanov (1953) was the first to postulate hybridization between *Platyceps* karelini and P. rhodorachis. This assessment is based upon specimens from the Murgab Valley (SE Turkmenistan) combining the diagnostic features of *P. karelini* (presence of a posterior subocular, i.e., a single supralabial in contact with eye) and the typical phenotype of *P. rhodorachis* showing a reddish vertebral stripe from the nape all along the trunk. Both character states are observed in ZMB 38833 from the Garagum (Karakum) Desert (Fig. 6A, Tb. 4). This female has two superposed loreals (upper smaller, actually the split off lower lateral edge of the prefrontals) and, on the left side, a divided preocular, a presubocular, a narrow cuneiform scale separating the upper portions of the second and third supralabials, and eleven sublabials; the posterior chin shields are separated by four (cranial, instead of the usual two) to five (caudal) rows of elongate scales. Besides a faint reddish median line on a uniform light brownish dorsum, there are a few tiny scattered dots along the back. Furthermore, we absolutely consider BMNH 1886.9.21.104 (&, Fig. 7A, Tb. 4) from Herat Province (Gulran, see Distribution) with a posterior subocular and a bright orange vertebral stripe to be a hybrid of *P. karelini* and *P. rhodorachis* (see next but one smallprint) ⁷⁾. It has a small supplementary dorsolateral head scale, i.e., the detached posterior outer edge of the internasal. Boulenger (1889), apparently in a quandary, first assigned this "very fine specimen [...] splendidly marked with a bright red broad line down its back" to rhodorachis but referred to it later as karelinii [sic] (Boulenger, 1893: letter h, " \updownarrow "). All subsequent reports regarding the presence of a reddish median stripe in karelini from the area under consideration (e.g., Smith, 1943; Mertens, 1969: 59; Clark, 1990), i.e., except regions within the former Sovjet Union, rely upon this male from northern West Afghanistan.

Viable crossbreeds between *Platyceps karelini* and *P. rhodorachis* do not appear to be uncommon in certain areas of sympatry, in particular Southeast Turkmenistan (e.g., Bogdanov, 1953, 1962; Czellarius, 1974, 1992; see footnote 8) and adjacent Afghanistan (Figs 6A, 7A). Although the topic needs further investigations (in prep.) including fieldwork and intricate molecular techniques, recombinations involving the hybrid genome may result in a disordered genetic equilibrium reflected in, for example, aberrant morphology. As one of the parent species (*P. rhodorachis*) features two distinct phenotypes (uniform with longitudinal vertebral stripe versus transversely blotched or spotted dorsal pattern), it seems reasonable to assume that different colour morphs also occur in *P. karelini* x *P. rhodorachis*. This is why we speculate that the

⁷⁾ On the right side, BMNH 1886.9.21.104 shows a split off triangular portion (lower anterior edge) of the seventh supralabial and the comparatively narrow upper anterior temporal extends as far caudal as the lower (Fig. 7A) whereas this scale is distinctly shorter (and much smaller than the lower first temporal) on the left as is often the case in *Platyceps karelini* (Figs 4, 10A). A long slender upper anterior temporal is also found in TMUS 1001 (W Iran); it is longer than usual in ZMB 38591 (left side, Tadzhikistan) and a Turkmen racer (ZMB 38816, see Northern Populations and last paragraph of this chapter).

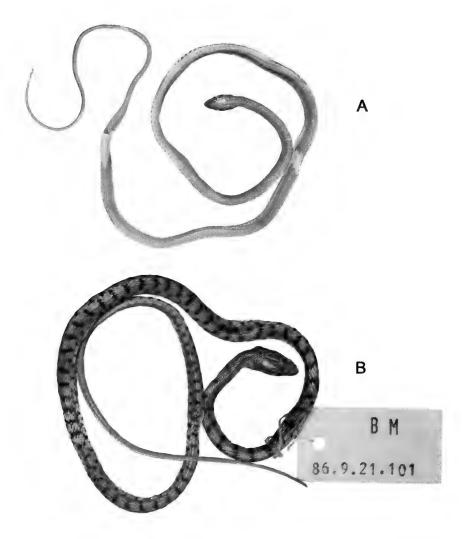


Fig. 6

Dorsal view of *Platyceps karelini* x *P. rhodorachis* from Turkmenistan (A, ZMB 38833, Garagum Desert) and a supposed Afghan hybrid racer (B, BMNH 1886.9.21.101, Nimruz, see text, Appendix A). Not to scale.

holotype of *Choristodon brachycephalus* Severczov (ZISP 3581) showing a blatant deformation of the head is, if not a teratism, an abortive hybrid (see footnote 4).

BMNH 1873.1.7.10 (Fig. 8, juv. 3) has a minuscule left presubocular and a colour pattern reminiscent of *Platyceps karelini* (Figs 1, 9A, see Comparison: first smallprint). It is remarkable for various head and body scale conditions, e.g., the shape of the loreal (higher than long), orbit completely separated from supralabials by three suboculars (fifth supralabial horizontally divided, lower portion distinctly smaller), number and arrangement of sublabials (ten and only three in contact with anterior chin

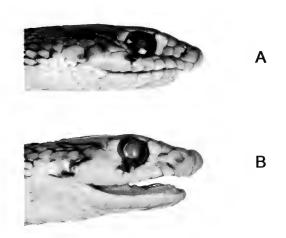


Fig. 7

Rostral shape and right lateral head scales of *Platyceps karelini* x *P. rhodorachis* (A, BMNH 1886.9.21.104, Herat) and a potential hybrid between these species (B, CAS 120540, Balkh) from Afghanistan. Courtesy of Philippe Wagneur (A). Not to scale.



Fig. 8

Dorsal and left lateral head views of BMNH 1873.1.7.10, a *Platyceps karelini* x *P. rhodorachis* from Afghanistan (Nimruz: Qala-i Fateh).

shield on one side, eleven and four, respectively, on other) as well as a much elevated number of ventrals and total body scales compared to males from the whole range and both genders of southern *P. karelini*, respectively (Tbs 3-4). These character states and meristic data prompt us to classify this racer obtained near the Afghan-Iran border as a hybrid (*P. karelini* x *P. rhodorachis*).

BMNH 1873.1.7.10 (coll. Major Euan Smith) from "Kila-i-Fath, Sístán" (Qala-i Fateh, NW Nimruz) has "all the labials below the eye divided", 216 ventrals, and 107 subcaudals (Tb. 4), pretty close to Blanford's (1876) counts ("ventrals are 218 in number, subcaudals 108", see footnote 2). Boulenger's (1893) data for this specimen (207 and 99, respectively) are incorrect. Two *Zamenis ventrimaculatus* [sic] sensu Blanford (1876) are discussed elsewhere (Systematics: first smallprint); BMNH 1873.1.7.10 and probably one of the three Kerman racers (see below; this series includes ZSI 4615, see Sclater, 1891: as *Z. ladaccensis* [sic], i.e., *Platyceps rhodorachis*) also enumerated by Boulenger (1893) are *P. karelini* x *P. rhodorachis*. Four out of seven *Z. karelini* sensu Boulenger (1893) from Kerman and Afghanistan including BMNH 1886.9.21.104 (see above) and probably 1886.9.21.101 (below) may be hybrids, and there is actually no verified record of genuine *P. karelini* from Southwest Afghanistan (Fig. 5: arrow).

TABLE 4. Body scales (number of ventrals, subcaudals, and sum; extreme tip of tail possibly missing in ZMB 38833), dorsal scale row (dsr) reductions (longitudinal position in %ven, transverse level), and dorsal markings (patterned [transversely blotched or spotted] or striped phenotype) of *Platyceps karelini* x *P. rhodorachis* and three supposed or potential hybrid racers (preceded by an asterisk; see text, Figs 5-8 and Tb. 1 for definitions).

Specimen	Ventrals, subcau- dals and sum		Reduction pattern (dsr) in %yen transv. levels		Phenotype	Gender and country (province)	
	dais	and si	AIII	III 70VeII	transv. ieveis		(province)
BMNH 1873.1.7.10	216	107	323	59, 60, 75	par - lat - par	patterned	♂, Afghanistan (Nimruz)
*BMNH 1874.11.25.10	203	102	305	59, 61, 70	(see text) - par	patterned	♂, Iran (Kerman)
*BMNH 1886.9.21.101	203	105	308	61, 62, 79	par - lat - par	patterned	ೆ, Afghanistan (Nimruz)
BMNH 1886.9.21.104,	206	110	316	57, 63, 77	par - lat - p+v	striped	♂, Afghanistan (Herat)
*CAS 120540	207	105	312	56, 63, 71	par - lat - par	patterned	♂, Afghanistan (Balkh)
ZMB 38833	212	110?	322?	59, 65, 71	par - lat - par	striped	♀, Turkmenistan (Mary)

BMNH 1874.11.25.10 from Kerman (see smallprint above, Material and Methods, Schätti & Schmitz, 2006: 761) differs vis-à-vis Iranian *Platyceps karelini* in its number of complete transverse dorsal blotches, i.e., more than 55 compared to 41-50 except in an unexamined specimen from Qom (Fig. 1, see Comparison). The cross-bands become narrow towards midbody and it seems that the posteriormost portion of the trunk is devoid of any dorsal pattern (or mid-dorsal transverse markings faded away) which is atypical of *P. karelini* but characteristic of *P. rhodorachis*. We suppose this racer with a noteworthy dorsal scale row sequence (reduces to 17 dsr on the right side involving low and high levels and then to 15 dsr on the left) and BMNH 1886.9.21.101 from the Arghandab (Helmand, see Material and Methods) in Nimruz to

be hybrids. The latter, from an area where *P. karelini* may be syntopic with *P. minto-norum* (Fig. 5, see Comparison), has over 70 consistently narrow transverse bars all along the dorsum (Fig. 6B) compared with 50 or less in specimens from Iran to probably as far west as at least 53°E longitude (see above). Furthermore, CAS 120540 from North Afghanistan with about 78 short cross-bands is considered a *P. karelini* x *P. rhodorachis* hybrid. It is outstanding compared to southern (and most northern) *P. karelini* studied by us for its condition of the preocular (divided, Fig. 7B) and a single right anterior temporal (unique among examined material) as well as further unilateral head scale features, i.e., an elevated number of supralabials (ten) and eleven sublabials. Certain reservations regarding the hybrid nature of this racer arise from the lack of data for genuine *P. karelini* from North Afghanistan (Fig. 5), a similar number of dorsal markings in contiguous northern populations, and the occurrence of two preoculars in MTKD 16095 from adjacent Tadzhikistan (see Morphology: third smallprint, Northern Populations).

The rostral of CAS 120540 is noticeably protruding and it is slightly so in BMNH 1886.9.21.104 (*Platyceps karelini* x *P. rhodorachis*, Figs 7A-B). The conspicuously projecting snout of the latter is due to a crushed mandible. Although the muzzle clearly projects beyond the lower jaw in some *P. karelini* (e.g., BMNH 1886.9.21.102 and USNM 148631, both with a remarkably pointed snout in dorsal, or ventral, view), this condition is subject to variation and does not allow a distinction from, for instance, *P. rhodorachis* (contour of snout in dorsal view inconstant to some degree as well). Moreover, the rostral of BMNH 1886.9.21.104 and, for example, CAS 120540 is deeply wedged in between the internasals (see footnote 4). At least in *P. karelini*, the shape of the posterior dorsal edge of the rostral is an unstable character, resulting in variable proportions of the anterior snout scales. This is exemplified by SMF 62924 and 62940 (both specimens show a surprisingly blunt anterior edge of the rostral in dorsal view) with distinctly longer internasals (measured along median suture) versus BMNH 1886.9.21.102 (Fig. 2A) or MNHN 1999.8160 which have the rostral wedged in between the internasals and comparatively much longer prefrontals.

Except for BMNH 1874.11.25.10 and 1886.9.21.101, specimens discussed in this chapter display peculiarities of head scales, maybe to the point of anomalies (ZISP 3581), and possibly other characters. It cannot be ruled out that our samples of *Platyceps karelini* (Appendices A-B) comprise a few additional hybrid racers. Possible candidates are ZMB 38816 from the Turkmen-Iran border (Tedzhen) with a much elevated number of cross-bands (ca. 65, see Northern Populations incl. second small-print) and NMW 25446.2 (\$\frac{1}{2}\$, 210 ventrals, 104 subcaudals) from the Murgab Valley with coalesced frontal and parietal shields, eleven left sublabials, and about 55 comparatively narrow transverse dorsal bars (posteriormost short) with straight anterior and posterior borders instead of the typical slightly rounded contour as shown by a male *P. karelini* (NMW 25446.1) from the same area (see footnotes 6-7).

COMPARISON

With the exception of *Platyceps mintonorum* (Mertens), Karelin's Racer differs from most congeneric taxa, and in particular all sympatric species, in the presence of a posterior subocular scale, i.e., a single (usually fifth) supralabial in contact with the eye (rarely none) versus two in Southeast Mediterranean and Saharo-Sindian *Platyceps* spp. Besides the condition of the suboculars (e.g., Strauch, 1873; Boulenger, 1893; Werner, 1929; Leviton & Anderson, 1970; Khan, 1997), *P. karelini* (Brandt) is charac-

terized by a conspicuous oblique streak below the eye and another on the temple as well as dark dorsal cross-bands all along the trunk persisting in adults (Minton, 1966; Mertens, 1969; Khan, 1997). These markings separate *P. karelini* from any taxon dealt with in the present study except Chesney's Racer. *P. najadum* (Eichwald, 1831), sympatric with Karelin's Racer from western Iran to Golestan, northern Khorasan-e Razavi, and the Kopetdag piedmont ⁸⁾, differs from all discussed species in the number of apical pits (single versus paired) and further morphological characters including the dorsal colour pattern (Schätti *et al.*, 2005).

The occurrence of striking dark transverse dorsal blotches in *Platyceps* spp. other than Karelin's and Chesney's Racers is observed in juveniles of, for example, P. ventromaculatus (Khan, 2006: Pl. 136B). Regarding the dorsal colour patterns of the taxa discussed in this paper, the reader is referred to the following selection of photographs and other illustrations. Coluber chesneii Martin: Leviton et al., 1992: Pl. 15F; Khan, 1993: Fig. 13, 1997: Fig. 3, and 2006: Pl. 123 (see Morphology: third smallprint); Schätti, 2006: Pl. 1; Yildiz, 2011: Figs 2 and 3a; or the excellent engraving of the destroyed MSNM syntype of Zamenis persicus Jan in Jan & Sordelli, 1867: Pl. II.1 (see Conclusions: smallprint, footnote 10). P. karelini: Nilson & Andrén, 1981: Abb. 9; Khan, 2002: Figs 41-43 (see chresonyms); or Strauch, 1873: Pl. III (incl. dorsal view of a syntype) and Latifi, 1991, 2000: Fig. 34 (coloured drawing). P. mintonorum: Minton, 1966: Pl. 24.2; Mertens, 1969: Abb. 17 (holotype); Khan, 2002: Fig. 64 ("Coluber rhodorachis", also published mirror-inverted in Khan, 1993: Fig. 22); Schätti & Stutz, 2005: Pl. 1. *P. rhodorachis*: Minton, 1966: Pl. 25.1 (reproduced in Khan, 2006: Pl. 134); Leviton et al., 1992: Pl. 15E; Khan, 2002: Fig. 66; or Bannikov et al., 1977: Pl. 28.4-4a and Latifi, 1991, 2000: Figs 41-42 (coloured drawings). P. ventromaculatus: Minton, 1966: Pl. 24.1; Leviton et al., 1992: Pl. 15H; Khan, 2002: Fig. 67; Khan, 2006: Pls 136A-B; Schätti & Schmitz, 2006: Fig. 1.

Platyceps mintonorum is an endemic racer of Baluchistan (Fig. 5) documented from Afghanistan and Pakistan; according to Latifi (1991, 2000) it also occurs in "Sistan and Baluchistan Province (Zabol, Zahedan)". There, as well as in Nimruz, at Chah-i Anjir (Helmand) or near Kandahar, this species and P. karelini may be syntopic (see Systematics: first smallprint, Hybrid Racers). Minton (1966) emphasized that the 'Variegated Sand Racer' (i.e., P. mintonorum) "is distinct from ventromaculatus, rhodorachis, and karelini in the regular presence of a third preocular [see Morphology: first smallprint], high ventral count, and body pattern", and that karelini and mintonorum "are quite different in pattern and in ventral and subcaudal counts." In fact, Mintons's Racer differs in various morphological characters including the number of preocular scales (entire in southern and most other karelini, often divided in mintonorum), more ventrals (221-240), subcaudals (110-127), and total number thereof (336-360, Schätti & Stutz, 2005) compared with 196-212, 90-106, and 288-314, respectively, in P. karelini from Iran to Pakistan (Tb. 3, see Morphology: second small-print).

Platyceps rhodorachis (Jan) is distributed over most of Iran, Afghanistan and Pakistan except in truly arid country and sandy areas or at high altitudes. The typical phenotype of *P. rhodorachis* can easily be distinguished from *P. karelini* by its reddish vertebral stripe running all along the dorsum. The condition of the supralabial scales

⁸⁾ "This lowland snake species [*Platyceps karelini*] is very rare" along the southern foothills of the Kopetdag in adjacent Turkmenistan (Atajev *et al.*, 1994). In Khorasan-e Razavi, *P. n. najadum* is recorded from, for example, Darreh Gaz (Dargaz, Latifi, 1991) and the Kuh-e Qamar Ali area (37°27'48"N 58°38°04"E, above 2'000 m a.s.l., TMUS specimen).

beneath the eye (see above) allows instant distinction from the striped and patterned (transversely blotched or spotted) morphs of *rhodorachis*. Furthermore, the dorsal colour pattern of the latter phenotype fades away behind midbody. Jan's Cliff Racer usually lacks a posterior subocular (two supralabials enter the orbit). The occurrence of this scale in *rhodorachis* is definitely a rare condition; a posterior subocular seems to be present in a specimen from Central Punjab assigned to *karelini* (Khan, 1977) due to a single supralabial in contact with the eye. However, this racer belongs to *rhodo-rachis* as evidenced by the number of subcaudals (130) and its origin (see Distribution: second smallprint).

"The nearest relative to *karelini* appears to be *ventromaculatus*; the two differ only in the regular presence of a third postocular in *karelini* [see Morphology: first smallprint], in head markings, and in the stronger blotched pattern of *karelini*" (Minton, 1966: 123). Although this observation including the remark regarding the head markings, and in particular the occurrence of a nuchal streak in *Platyceps ventromaculatus*, is correct, there is no substantial evidence of a sister species relationship and the posterior subocular (present or absent) is a variable character in Gray's Racer (Schätti & Schmitz, 2006). *P. ventromaculatus*, a lowland species from Northwest India and Pakistan, does not extend west of the Indus Valley except along the Baluch coast and is geographically separated from *P. karelini* (Fig. 5, see Systematics).

Platyceps karelini and Coluber chesneii Martin meet on the Central Plateau (Iran), the closest known records being from about 80 km southeast of Esfahan and the eastern foreland of the central Zagros Range (Izad Khvast, Fig. 5, see Conclusions). Chesney's Racer is confirmed from the Arvand Rud (Shatt Al-Arab, Khuzestan) area and along the frontier with Iraq to at least as far north as Kermanshah (e.g., MHNG 1359.12). It probably occurs in Kurdestan Province and may encroach upon the eastern escarpment of the Zagros (Semirom District in extreme SW Esfahan, Chahar Mahall-ve Bakhtiyari) or extend eastward down the southern Zagros and across the foothills inland from the Gulf littoral. C. chesneii M. covers a considerable altitudinal range from near sea level (Bushehr and Khuzestan) to roughly 2'200 m in northernmost Fars (FMNH 20939). FTHR 15300 was collected in the same general habitat as P. najadum (ssp.), i.e., rocky terrain with scattered oak forest between 600-1'100 m in North Khuzestan (Torki, 2010: 30-31, Fig. 10, as P. karelini).

A Zamenis ventrimaculatus [sic] "Var. A. v. Günther" from "Borazjûn" (Borazjan, 29°16'N 51°12'E) in Bushehr Province (Werner, 1917: 211) obtained by Friedrich Carl Andreas could not be located in institutional collections rummaged through by us. Field notes of the collector contain three "Z. v. var. D. persica" from "Tangistân" near Ahram (Bushehr) and a cottage at "Tschâbâgh", possibly in Fars; these specimens were not accessible to Werner (1917) and probably belong to Platyceps rhodorachis (Schätti et al., 2010: 278). Raï's (1965: map 9) unspecified record of "Coluber karelinii" [sic] from the Kermanshah-Iraq border area is based upon Chesney's Racer as evidenced by the low number of supralabials ("Labiales supérieures 8 (quelquefois 9)"), as sometimes observed in this taxon (Schätti, 2006), and their condition relative to the eye, i.e., two supralabials in contact with orbit (l.c.: 44-45).

Except for FMNH 20939 (Fig. 10B) and NMW 25446.7 (with a right presub-ocular, Fig. 10C), Iranian *Coluber chesneii* M. examined by us have nine supralabials and usually the fifth and sixth in contact with the eye. In BMNH 1869.8.28.130, the right fifth supralabial is horizontally divided (lower part excluded from orbit) and a

presubocular is present on the left side 9). NHMB 15210 has a narrow upper portion of the anterior subocular split off (the posterior part of this scale is above the lower border of the eye; this condition could be described equally well as a 'divided preocular') and a tiny subtriangular presubocular, i.e., the detached lower posterior edge of the loreal. There are 204-217 ventrals (3.204-217, 9.206-208, 209 in FMNH 20939), 101-116 subcaudals (102-116, 101, and 110, respectively), and a sum of 307-333 (310-333, 307, 319, resp.). Four males (BMNH 1869.8.28.130, FTHR 15300, MHNG 1359.12, MNHN 7470) have considerably fewer ventrals (204-209) and total body scales (310-318) than NMW 25466.1 (Fig. 9C) and SMF 61869-70 (3.214-217, 323-333, resp.) from unspecified localities in Iran. The number of maxillary teeth ranges from 13-16 (n=7); the maximum is from the extant syntype of *Zamenis persicus* Jan (see next smallprint).

Apart from the number of supralabials entering the eye and body scales (see above, following paragraph, next chapter, and Tb. 3), Chesney's and Karelin's Racers differ in their dorsal colour patterns. Authentic *Coluber chesneii* M. display characteristic markings on the pileus which persist in adults, possess a nuchal streak (Jan & Sordelli, 1867: Pl. II.1), and have more than 60 transverse bars along the dorsum (see Comparison). Furthermore, this taxon seems to attain larger body size as exemplified by NMW 25446.7 (\mathcal{P} , ca. 100 cm total length, Fig. 9B) and, possibly, Latifi's (1991, 2000) maximum dimension for *C. karelini* auct. (see Morphology). Besides this, Chesney's and Karelin's Racers are very similar regarding their general habitus, scale features, and further morphological characters. They show, for instance, the same range of maxillary teeth (13-16) and virtually identical hemipenes, in particular with respect to the fringe of tiny spines along the sulcus spermaticus (Fig. 3; Schätti, 2006: Fig. 1).

Three *Platyceps karelini* from Markazi (RUZM 11.1, $\,^{\circ}$, tail broken), Esfahan (USNM 240003, $\,^{\circ}$, 103 subcaudals), and Qom (unregistered, tail truncated) have 204 ventrals each, which is the minimum ascertained in Chesney's Racer from Iran ($\,^{\circ}$ $\,^{\circ}$). USNM 240003 possesses the same number of total body scales (307) as NMW 25446.7 ($\,^{\circ}$, see next chapter). Most *P. karelini* are devoid of dorsal head markings and usually lack a nuchal streak. It is, however, present in a QDE male (Fig. 1) and a middorsal spot behind the parietals occurs in all three examined specimens from Southwest Esfahan, Markazi, and Qom. These four *P. karelini* show approximately 45-52 crossbands along the trunk (see Morphology: third smallprint). The posterior edges of the

⁹⁾ BMNH 1869.8.28.130 from "Bushire" (Bushehr, "Dr. Leith") unquestionably belongs to Chesney's Racer. However, this collector obtained his material (e.g., BMNH 1869.8.28.116, 1869.8.28.132 and 134) from "Kurrachee" and "Sind" (Boulenger, 1893: 400, letters n and p-s; Schätti & Schmitz, 2006: 768), and there seems to exist confusion regarding the origin, provenance, and published data of BMNH 1869.8.28.130 (*Coluber chesneii* Martin) and 1879.8.15.27. The former (Boulenger, 1893: letter f) has a truncated tail with 90 subcaudals instead of "92". BMNH 1879.8.15.27 (Blanford, 1881; Boulenger, 1893: letter g) is a female with 205 ventrals, 110 subcaudals (Schätti, 2006: footnote 1), and 19-19-14 dsr registered as from "Bushire, Persia". This specimen, purchased from dealers of natural history items (Watkins & Doncaster), lacks dark markings on the pileus, and the transverse dorsal bands (becoming indistinct and confined to the vertebral area towards the tail) show irregularly serrated anterior and posterior borders. This racer belongs to *Platvceps ventromaculatus* (Gray).

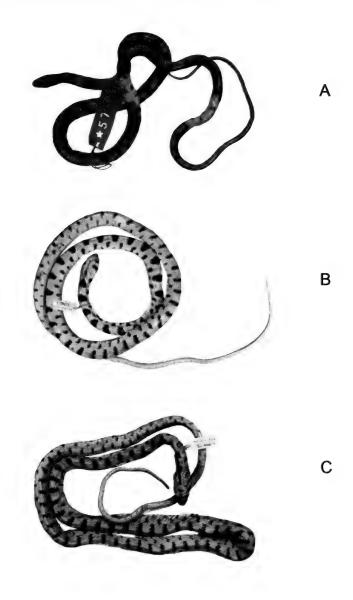


Fig. 9

Dorsal view of Iranian *Platyceps karelini* (A, MNHN 1957.60, Serakhs) and *Coluber chesneii* Martin: NMW 25446.7 (B, "Schiraz" intergrade, see Fig. 10C) and NMW 25466.1 (C, "Persien"). Courtesy of Ivan Ineich/MNHN and Heinz Grillitsch/NMW. Not to scale.

frontal are darkened except in RUZM 11.1 (with two indistinct longitudinal dark stripes instead); the latter and USNM 240003 (Fig. 2C) disclose a blurry blotch across the supraocular; RUZM 11.1 exhibits cloudy pigmentation on posterior portion of the parietals.

CONCLUSIONS

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Morphology (pholidosis, dentition, hemipenis) substantiates that *Platyceps* cf. *ventromaculatus* sensu Schätti (2006) from Northeast Africa to Iran, i.e., *Coluber chesneii* Martin (see Systematics incl. second smallprint), is conspecific with *P. karelini* (subspecies). The seemingly parapatric distribution of *P. k. karelini* (Brandt, 1838) and *P. karelini chesneii* (Martin, 1838) comb. n. as well as the existence of overt intergrades corroborate this new systematic concept.

The specific name karelini has priority over chesneii because Brandt's (1838) description was published beginning of February ("Emis le 2 Février 1838") as notified on the last page (col. 256) of number 16 ("tome troisième") of the 'Bulletin scientifique [...]' whereas Martin's (1838) report on the 'Euphrates expedition' was delivered in July of that same year (Sclater, 1893). The type series of Coluber chesneii Martin from the "Euphrates" presented to the Geological Society of London (Chesney, 1850) consisted of several individuals but a single adult female syntype (BMNH 1946.1.12.95) is known to be deposited in an institutional collection (Günther, 1858, 1864; Boulenger, 1893; Schätti, 2006). Apart from the original description, references to C. chesneii M. are found in Günther's (1858, 1864) 'Catalogue' under "Var. A" of Zamenis ventrimaculatus [sic] and 'The reptiles of British India' ("A specimen [...] from Mesopotamia", i.e., the extant syntype, "agrees completely with the types" of C. ventromaculatus Gray), as a valid species (Z. chesnei [sic], Günther, 1868; see also Günther, 1874) or in the synonymy of Z. ventrimaculatus [sic] auct. (Stoliczka, 1872; Blanford, 1876; Boulenger 1890, 1893; Wall, 1914; again as chesnei [sic]) as well as in Sherborn (1925), Schätti (2005: 170, 172, 174; 2006), Schätti & Schmitz (2006, see Systematics: second smallprint), and in Schätti et al. (2010) who declared the junior synonym Zamenis persicus Jan, 1863 a nomen oblitum.

FMNH 20939 and NMW 25446.7 from the Fars-Esfahan border and "Schiraz" ¹⁰⁾ are the only specimens out of about 175 "*Platyceps* cf. *ventromaculatus*" examined by the senior author (Schätti, 2005, 2006) with a posterior subocular, i.e., a single (sixth or fifth, respectively) supralabial entering the orbit (Figs 10B-C, see Comparison regarding the condition in BMNH 1869.8.28.130). They were collected in the area of contact with *P. k. karelini* (Fig. 5) and have more than 60 transverse dorsal bars as typically found in *P. k. chesneii* but the markings on the pileus characteristic of this taxon are absent; the subadult (FMNH 20939) also lacks a nuchal streak whereas NMW 25446.7 (Fig. 9B) shows a stripe along the nape and a black interparietal line (as well as dark posterior edges of the frontal) as often found in *k. karelini*. Manifestly, these two racers are intergrades with the nominotypical subspecies. They also deviate from the normal number of supralabials (nine) observed in Chesney's and Karelin's Racers (eight on right side of unregistered Qom specimen, see remark in Appendix A), i.e., eight (NMW 25446.7, right) and ten (FMNH 20939, Figs 10B-C).

The eastern portion of the species' range is inhabited by *Platyceps k. karelini* (see Distribution). *P. k. chesneii* is recorded from Southeast Turkey (e.g., Yildiz, 2011) through the Euphrates Valley to Iran (eastern escarpment of central Zagros) and the northern Arabian Peninsula (NE Saudi Arabia, Kuwait, Bahrain) including Sir Bani Yas

¹⁰⁾ "Schiraz" must be interpreted in its broadest sense; specimens with that origin (e.g., destroyed MSNM syntype of *Zamenis persicus* Jan or NMW 25446.7) were collected during a time when this appellation or "Shirâz" were used virtually synonymous with today's Fars Province. With reservations, these records are arbitrarily mapped at 29°37'N 52°32'E, ca. 1'520 m a.s.l. (Fig. 5). The collector of NMW 25446.7 is not registered; this is probably the former 'Indian Museum' specimen "given to Dr. F. Stoliczka" (Anderson, 1872; see Schätti *et al.*, 2010).

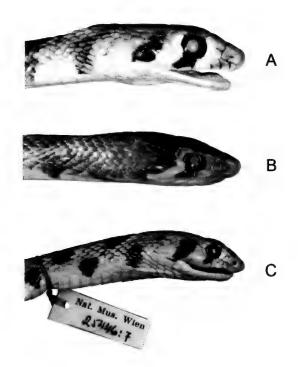


FIG. 10

Right lateral head view of Iranian *Platyceps karelini* (A, USNM 240003, see Fig. 2C) and intergrades with *Coluber chesneii* Martin (i.e., *P. karelini chesneii*): FMNH 20939 (B, subadult) and NMW 25446.7 (C, see Fig. 9B) showing a posterior subocular and ten or eight, respectively, supralabials; USNM 240003 and NMW 25446.7 with a presubocular (see text). Courtesy of Alan Resetar/FMNH and Heinz Grillitsch/NMW. Not to scale.

Island (UAE, Fig. 5) ¹¹⁾. The actual distribution limits in Iran (see Comparison) and the potential occurrence in Qatar require specific investigations.

Populations of *Platyceps* cf. *ventromaculatus* sensu Schätti (2006) from southern Syria and Jordan to eastern Libya (Cyrenaica) are referred to *P. karelini rogersi* (Anderson, 1893) comb. n. The validity of Rogers's Racer relies entirely upon differences in dorsal colour pattern, i.e., the transverse blotches considerably wider than interspaces (e.g., Disi, 2002: three unnumb. photographs; Disi *et al.*, 2001: Figs 190-191; Schätti, 2005: Fig. 1; Amr & Disi, 2011: Fig. 72) versus cross-bands narrower

¹¹⁾ Various reports of *Coluber ventromaculatus* auct. from the United Arab Emirates (e.g., Hornby, 1996; Drew *et al.*, 2005; Gardner, 2009) remain unspecified as to the source of information or voucher specimens. We are not aware of any verified record except for Sir Bani Yas Island (24°20'N 52°36'E) documented by, for example, NMW 32192 (Brown, 1991; Tiedemann, 1991: Figs 2-3; Schätti, 2006; see also Gardner, 2005). Most probably, this racer had been introduced into that island by human activity. The identity of the Sir Bani Yas population (i.e., *Platyceps chesneii*) is further substantiated by a living specimen photographed by Simon Aspinall (picture provided by Andrew Gardner).

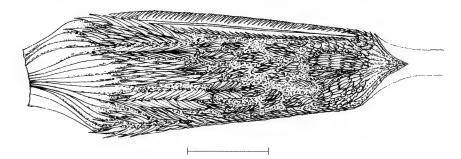


Fig. 11

Left in situ hemipenis of *Platyceps karelini rogersi* HUJ 3185 from Jordan. Scale equals 5 mm. Drawing Heidi Laubscher.

(or, at best, equal to interspaces) in *P. k. chesneii* (Figs 9B-C, see Comparison: first smallprint). The hemipenis of *P. k. rogersi* (Fig. 11) coincides in all structural details with the remaining subspecies and the sister taxon relationship of Karelin's and Rogers's Racers is supported by molecular data (see Systematics).

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Appendix A

Platyceps k. karelini and hybrid racers from Iran to Pakistan examined (see Material and Methods for approximate coordinates and altitudes; specimens preceded by an asterisk were used for the calculation of cephalic indices; only head and body scale counts available in the case of PMNH specimens [2] and limited data set for CAS 84636 and NMW 25446.3; BMNH 1886.9.21.102-103 not individually labelled). P. k. karelini. AFGHANISTAN: BMNH *1882.3.20.2 (Kandahar, 31°37'N 65°42'E, ca. 1'000 m, &, pres. Col. Swinhoe), *1886.9.21.102 (Tirpul [Tir Pol], 34°36'N 61°16'E, 768 m, ♀, see remark above, Fig. 2A), *1886.9.21.103 ("Kilki", ca. 34°00'N 61°25'E [Ziarat-e Fateh Mohammad area], ca. 975 m, ♀, see remark above); CAS 84634-36 (Chah-i Ānjir, 31°40'N 64°19'E, ca. 800 m, ♀, juv. ♂ ♂, see remark above and Tb. 1), 103785 ("Herat to Islam Qala" [Islam Qaleh], ca. 34°30'N 61°17'E ["about 20 miles from the Iranian border", Kuh-e Chazirak area], ca. 800-950 m ["Elevation 3100 to 2600 feet": Clark et *al.*, 1969], ♀), 120714 (45 km west of Herat, ca. 34°25'N 61°45'E, 880 m [Clark, 1990], ♀); MNHN *8722 [juv.] and *1999.8160 [formerly 8722A] ("Ker Dahar" [Chahar Dahaneh], 31°38'N 65°39'E, ca. 1'000 m, &&, see Tbs 2-3); SMF *64629 (Darzi Chah, ca. 29°45'N 65°30'E, ca. 915 m, subad. ♂, coll. Jeromie A. Anderson). IRAN: FMNH *141604 ("25 mi. N Pahlavi Dezh" [Aq Qal'eh], ca. 37°25'N 54°27'E, nr.s.l., ♀); MHNG 2718.11 (Esfandiar [E Yazd], 33°02'N 57°33'E, ca. 1'400 m, d), 2718.12 (vic. Naseri, 36°10'N 57°33'E, ca. 900 m, ♂, coll. Ashgar Afzal Abadi); MNHN 1957.59 (Dashli Borun, 37°38'N 54°49'E, ca. 50 m, ♀, Fig. 2B), 1957.60 (Serakhs, 36°32'N 61°10'E, ca. 280 m, \$\partial\$, Fig. 9A); NMW 25446.3 (vic. Neh [Nehbandan], ca. 31°32'N 60°02'E, ca. 1'175 m, juv., see remark above and Tb. 1), *25446.4

("Zirkukh" ["Germau", Garmab], 33°53'N 59°42'E, ca. 1'155 m, ♀), *25446.5 (Gulu Chahak, 31°19'N 59°25'E, 980 m [Gabriel, 1938], \(\parple\), *25446.6 (Chah-e Sam, 30°43'N 60°03'E, 1'206 m [Gabriel, 1938], ♂); RUZM *11.1 (Kal-e Do Band River, ca. 33°52'N 50°48'E [SE Markazi], 1'700 m, \$\times\$); SMNS *2381 ("Baluchistan", \$\times\$, see Material and Methods); TMUS *994 (southern Tandureh National Park, ca. 37°20'N 58°47'E, ca. 1'550 m, ♀), *1000 (ca. 50 km north of Nosratabad, ca. 30°18'N 59°57'E, above 1'500 m, ♂), 1001 (vic. Kavir-e Lut, east of Tahi salt area, 32°07'N 57°53'E, ca. 700 m, juv.), *1002 (Dasht-e Kavir, 35°04'N 55°03'E, below 750 m, &); USNM *148631 (1 km south of "Isfadeh" [Esfeden], ca. 33°39'N 59°47'E, ca. 1'190 m, ♀), *240003 ("Esfahan, 80 km SE of', ca. 32°24'N 52°05'E, ca. 1'600 m, subad. ♀, Figs 2C, 10A); ZMB 6876 ("Mazandaran" [Golestan], ♂); unregistered (vic. Navaran, ca. 34°36'N 51°05'E [15-20 km roughly east of Qom], ca. 900 m, coll. H. Bostanji, examined by Khosro Rajabizadeh, colour pattern ascertained from photographs). PAKISTAN: AMNH *96219 ("near Pishin", ca. 30°35'N 67°00'E, ca. 1'535 m, 3), 96220 (2 miles east of Hanna, Urak Valley, ca. 30°15'N 67°10'E, ca. 2'000 m, ♂); PMNH 761 (Kalat, 29°01'N 66°35'E, 2'018 m, 3), 762 (Mastung, 29°48'N 66°51'E, ca. 1'700 m, 3); SMF *62924 (Khuzdar, 27°48'N 66°37'E, ca. 1'215 m [1'140 m fide Mertens, 1969: 88], 3), *62940 (Quetta, 30°12'N 67°01'E, 1'650 m, ♀). P. k. karelini x P. rhodorachis. Afghanistan: BMNH 1873.1.7.10 ("Kila-i-Fath, Sístán" [Qala-i Fateh, Qaleh-e Fath], 30°34'N 61°50'E, 490 m above sea level, juv. 3, "Gen. [Frederic J.] Goldsmid" [register entry, coll. Major Euan Smith], Fig. 8), 1886.9.21.104 ("New Gulran", 35°06'N 61°41'E, ca. 750 m, ♂, Fig. 7A); ?CAS 120540 (10 km west of "Tashkurgan" [Tashqorghan, Khulm], ca. 36°42'N 67°36'E, ca. 570 m, δ , potential hybrid, Fig. 7B). IRAN: BMNH 1874.11.25.10 (Kerman, ca. 30°17'N 57°05'E, ca. 1'760 m, &, supposed hybrid, see Material and Methods). P. k. karelini x Platyceps sp. AFGHANISTAN: BMNH 1886.9.21.101 ("Helmand" [River], ca. 30°17'N 62°03'E [Arghandab Rod near Chahar Burjak], ca. 500 m, juv. ♂, supposed hybrid with *P. mintonorum*, see Material and Methods, Fig. 6B).

Appendix B

Northern Platyceps k. karelini and P. k. karelini x P. rhodorachis examined (only limited data, usually number of ventrals and subcaudals, available for specimens marked with an asterisk). P. k. karelini. KAZAKHSTAN: MTKD 13602 (Mujunkum [Mojyunkum] Desert, Dzhambul, ♂); ZISP 13436 (Mangyshlak [Mangghyshlaq] Peninsula, ♀). KYRGYZSTAN: MHNG 2442.96-97 (Bishkek, ♀♀); MTKD 10450 ("Frunze" [Bishkek], ♀). TADZHIKISTAN: MHNG 2442.98 (Shahrtuz [Shaartuz], subad.); MTKD 11335 (Gissarskaya Dolina [Kafirnigan], ♀), 16095 (Shahrtuz, ♂); NHMB 21058 ("Boba Tag" [Mountains], juv.); ZISP *15811 (Leninabad, juv.; ventrals, suboculars); ZMB 38591 ("Tadschikistan", ♀). TURKMENISTAN: CAS 184636 (14,2 km southwest of Madau [Madaw], δ); FMNH 83961 (Krasnovodsk [Türkmenbaşy], $\mathfrak P$); MCZ 109902 (Repetek, δ); MHNG 1358.27 ("Krasnovodsk Plateau", δ); MTKD 8281, (Ashgabat, ♀); NMW 25446.1-2 (Murgab Valley, ♂♂, incl. possible hybrid, see footnote 5); SMF 18219 (Ashgabat, ♀), 18220 (Durun, ♀); ZISP 17214.1-2 (Kyzyl Arvat, ♀, juv.), 17219 (Bajram Ali, 3), 17386 (Kyzyl Arvat, 3), 17582 (Kushka, 3), 18625 (Krasnovodsk, ♀), 19031.1-2 (vic. Garrygala [Karakala], ♀♀), ZMB 38816 (Sarahs ["Seraks"], ♀, possible hybrid). UZBEKISTAN: MHNG 2442.99-100 and 2443.01 (vic. Tashkent, ♂♂), 2443.03 (Bukhara [Buxoro], ♂); MTKD 13944 (Bukhara, juv.); ZISP *12907 and *13110 [incl. msr] (Tirmiz [Termez], subad., ♀), 14741 (Karakalpakstan, ♀), *17682 (G'uzor [Guzar], juv.; ventrals, suboculars). ORIGIN UNSPECIFIED: NHMB 7572 ("Transkaspien", ♀). P. k. karelini x P. rhodorachis. Turkmenistan: ZMB 38833 ("Kara-kum" [Garagum] Desert, 50 km east of Imambaba, \mathcal{P} , Fig. 6A).

Appendix C

Coluber chesneii Martin (i.e., Platyceps karelini chesneii) from Iran examined (includes two intergrades with P. k. karelini; no body scale data available for ZFMK 31602; NMW 28932.1 [Ash Sharqat, 35°30'N 43°15'E] is from Iraq, not "Iran" [Schätti, 2006: Appendix]): BMNH 1869.8.28.130 (Bushehr, 28°58'N 50°50'E, near sea level, ♂, see footnote 9); FMNH 20939 (Izad Khvast [Yezd-e Khast], 31°31'N 52°07'E, ca. 2'200 m a.s.l., subad. intergrade,

Fig. 10B); FTHR 15300 ("Tang-e Sat", near Nim Istgah-e Kornas railway station, N Andimeshk District, 32°52'N 48°44'E, 600-1'100 m [Torki, 2010: 30], ♂, examined by Farhang Torki, lateral head scale conditions and colour pattern ascertained from photographs); MHNG 1359.12 (east of Khosravi, ca. 34°23'N 45°29'E, ca. 250-280 m, ♂); MNHN 7470 ("en Perse", ♂ syntype of *Zamenis persicus* Jan); NHMB 15210 (Susangerd, 31°34'N 48°11'E, nr.s.l. ♀); NMW 25446.7 ("Schiraz", ♀ intergrade, see footnote 10, Figs 9B, 10C), 25466.1 ("Persien", ♂, Fig. 9C); SMF 61869-70 ("Iran", ♂♂); ZFMK 31602 ("Shirâz [...] oder [...] Buschähr" [Bushehr; Werner, 1917], juv.).

Nouvelles données sur la répartition de la souris des moissons (*Micromys minutus* Pallas, 1771) en Suisse occidentale et implications pour la gestion de son habitat

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New data on the distribution of the Harvest mouse (Micromys minutus) in western Switzerland and conclusions for the management of its habitat. - Knowledge about the distribution of the Harvest mouse (Micromys minutus) in western Switzerland has been completed by search for typical nests in the field. The authors visited formerly known sites and conducted a prospective search in new favourable habitat (sedge communities). Several new populations have been discovered in the canton of Jura and Vaud. Other sites have to be considered as abandoned, such as the region between the lakes of Bienne and Neuchâtel. Management measures in favour of the species are proposed.

Keywords: Harvest mouse - fragmentation - isolation - nest - western Switzerland.

Nouvelles données sur la répartition de la souris des moissons (Micromys minutus) en Suisse occidentale et implications pour la gestion de son habitat. - La répartition de la souris des moissons (Micromys minutus) en Suisse occidentale a été actualisée par la méthode de recherche des nids. Les auteurs ont procédé par contrôle des anciens sites connus et par prospections nouvelles dans les habitats favorables (cariçaies). Plusieurs nouvelles populations ont été mises en évidence dans les cantons du Jura et de Vaud. D'autres sont à considérer comme éteintes, comme dans l'Entre-deux-Lacs neuchâtelois. Des mesures de gestion favorables à l'espèce sont proposées.

Mots-clés: Souris des moissons - fragmentation - isolement - nids - Suisse occidentale.

INTRODUCTION

En Suisse, la souris des moissons (*Micromys minutus*) est une espèce caractéristique des prairies humides hautes, des zones marécageuses, des rives de cours d'eau et roselières (Rahm, 1995). Elle est intimement liée aux laîches à larges feuilles (*Carex* sp.) qu'elle utilise pour tresser son nid, mais peut accessoirement utiliser des graminées comme *Calamagrostis* sp. ou des céréales cultivées. Elle n'a pas été signalée en Suisse dans les milieux cultivés. En Europe, cette espèce a décliné dans de nombreuses régions en raison de la perte ou de l'altération des habitats par les drainages, l'assèchement des zones humides et l'intensification des pratiques agricoles (Mitchell-Jones *et al.*, 1999). Les champs de blé constituent son habitat principal en Grande-Bretagne, et les rizières dans le nord de l'Italie (Rham, 1995).

Plusieurs populations de souris des moissons (*Micromys minutus*) ont été localisées durant ces dix dernières années dans l'ouest de la Suisse, suite à des recherches ciblées en vue d'une amélioration des connaissances cantonales sur cette espèce et pour actualiser la Liste Rouge des mammifères terrestres. Ce petit rongeur, classé comme vulnérable dans la première Liste Rouge des mammifères de Suisse (Duelli, 1994), est probablement un des mammifères terrestres les plus menacés actuellement dans notre pays. Les données à son propos restent lacunaires et pas toujours fiables, les nids pouvant être confondus avec ceux du muscardin (*Muscardinus avellanarius*). De même, les critères de distinction crâniens sont ténus, et il y a des risques de confusion avec la souris domestique pour les crânes trouvés dans des pelotes de réjection de rapaces nocturnes (Marchesi *et al.*, 2008).

L'atlas des mammifères de la Suisse (Rahm in Hausser, 1995) signalait l'espèce à Genève, à l'ouest du lac Léman (La Versoix, Coppet), sur la rive sud du lac de Neuchâtel (Grande Cariçaie), dans l'Entre-deux-lacs entre Cressier et Le Landeron, sur la rive nord du lac de Morat et, plus au nord, à Bonfol et dans les environs de Bâle. La plupart de ces données, à l'exemple des cantons de Neuchâtel et du Jura, remontent à plus de 40 ans, soit entre les années 1960 et 1970. Durant les deux dernières décennies, la souris des moissons a été principalement observée dans la Grande Cariçaie. Elle y trouve certainement les conditions d'habitat les plus appropriées, et y développe sans doute la plus importante population du territoire suisse en raison de l'étendue de l'habitat disponible. En dehors de ce grand complexe marécageux, elle a tout d'abord été retrouvée dans le canton du Jura, grâce à l'identification d'un crâne dans une pelote de réjection de chouette effraie (Tyto alba) à Damphreux (Blant et al., 2003). Par la suite, des nids ont pu être observés sur le site des Marais de Damphreux en 2005, à l'occasion de relevés destinés à tester la méthode de mise en évidence de l'espèce, sur mandat du Centre suisse de cartographie de la faune (CSCF) (Blant et al., 2005). Des relevés plus systématiques y ont encore été effectués par la suite sur mandat de la Fondation des Marais de Damphreux, préalablement à des travaux de réaménagement, suggérant l'existence d'une importante population sur ce site (Blant, 2007). Ces résultats encourageants nous ont incités à vérifier le statut de cette espèce dans un contexte biogéographique élargi, à savoir la Suisse occidentale, afin de vérifier si les populations mentionnées par l'atlas subsistaient encore actuellement. L'objectif de cette publication est de présenter une synthèse des résultats des recherches dans les différents cantons concernés. Les études proposées devaient entre autres fournir des

indications sur le degré d'isolement des populations résiduelles détectées en dehors du complexe de la Grande Cariçaie, qui n'est pas discuté ici. La typologie des milieux occupés par la souris des moissons et leur état général ayant été relevés, l'article propose des recommandations pour un entretien des biotopes favorisant durablement le maintien de cette espèce menacée.

MATÉRIEL ET MÉTHODES

Les anciennes données (antérieures à 2002) ont été recherchées dans la base de données du CSCF, et par consultation des musées d'histoire naturelle (Musées d'histoire naturelle de Fribourg - MHNF, de Neuchâtel, de La Chaux-de-Fonds, Musée de Zoologie de Lausanne, Musée de la Nature de Sion, Musée des sciences naturelles de Porrentruy). Les données du Muséum d'histoire naturelle de Genève – MHNG, du Musée d'histoire naturelle de Berne – NMBE et de celui de Bâle – NMBA étaient déjà connues du CSCF pour l'élaboration de l'atlas. Des naturalistes des régions concernées, actifs dans le domaine des mammifères, ont également été contactés.

La mise en évidence des populations récentes (postérieures à 2002) de souris des moissons s'est faite par la recherche de ses nids. Cette méthode a été testée tout d'abord dans des biotopes d'où provenaient des observations (notamment Grande Cariçaie et région bâloise), en prévision de la révision de la Liste Rouge des mammifères terrestres (Blant *et al.*, 2005). Elle a été appliquée ensuite, dans un but essentiellement qualitatif (présence/absence), dans des sites parcourus pour leur potentiel d'habitat favorable. Dans quelques sites, une prospection quantitative a été faite de manière à pouvoir calculer un indice de population ou pour des questions relatives à la gestion du milieu. Une limite de surface minimale de 3 ares a été fixée pour la prospection des nouvelles surfaces potentielles. Les fragments de cariçaie inférieurs à cette dimension ont en général été écartés.

On peut succinctement résumer la méthode de détection comme suit:

- Parcours du site en automne (septembre à novembre) selon un ou plusieurs transects d'échantillonnage déterminés d'abord sur orthophoto, puis sur le terrain en fonction des caractéristiques végétales.
- Recherche à vue des nids dans les cariçaies, en écartant les touffes de laîches pour trouver les nids accrochés vers la mi-hauteur des plants.
- Recherche durant au moins 1 heure (½ h pour les plus petits sites) pour attester la présence/absence.
- Recherche dans le *Caricion (Carex acutiformis* ou autre), ou à défaut dans le *Phalaridion*, le *Phragmidion* ou la mégaphorbiaie à *Filipendula*.
- Photographie des nids et vérification de l'attachement au support, caractéristique du tressage de *Micromys* sur le matériel vivant (les nids de *Muscardinus* sont tressés avec du matériel coupé et sont posés sur un support, sans y être vraiment attachés) (voir Blant *et al.*, 2005)

Les prospections se sont limitées aux régions de plaine ou de vallées jusqu'à 700 m d'altitude, en raison de l'affinité de l'espèce pour ces niveaux altitudinaux (Rahm, 1995; Butet & Paillat, 1998).

RÉSULTATS

Vue d'ensemble

La souris des moissons a été localisée dans 21 sites situés du canton de Genève à celui de Bâle-campagne, jusqu'en 1990 (données des musées et CSCF, tableau 1). Par la suite, entre 1996 et 2001, de nombreuses captures ont été réalisées par le Groupe d'étude et de gestion (GEG) de la Grande Cariçaie, sur la rive sud du lac de Neuchâtel. Les animaux étaient piégés dans des seaux destinés au contrôle de la migration printanière des batraciens (A. Gander, comm. pers.). Des données extérieures à la Grande Cariçaie font par contre défaut entre 1990 et 2001.

Durant nos prospections opérées dès 2005, en dehors de la Grande Cariçaie, la souris des moissons a été retrouvée (tableau 2) dans 18 sites dans le canton du Jura (17 sites nouveaux + un site ancien), dans deux sites dans le canton de Vaud (nouveaux), et dans un seul site dans le canton de Fribourg (ancien). Dans le canton de Neuchâtel, aucun contrôle n'a pu permettre de déceler l'espèce, pourtant présente par le passé dans un site au moins. Dans le canton de Genève, aucun site potentiellement favorable n'a permis de retrouver l'espèce. Elle n'existe probablement pas dans le canton du Valais. Le Jura bernois n'a pas été prospecté en raison de l'altitude trop élevée.

La figure 1 présente la distribution exhaustive de l'espèce selon les données connues anciennes (jusqu'en 2001) et les découvertes récentes (jusqu'en 2011). La carte mentionne également tous les sites prospectés sans résultat positif.

TABLEAU 1. Données anciennes de *Micromys minutus* enregistrés dans la base de données du CSCF, situation jusqu'en 1990 pour la Suisse occidentale. Sites avec capture ou individu trouvé mort (type = 1), observations visuelles directes (type = 2) ou nids (type = 3), localités de mise en évidence par pelotes de réjection non mentionnées (situation exacte inconnue). Italique: observations douteuses (confusion possible avec *Muscardinus*).

Ct	Commune	Lieu-dit	Année	Type	Collection
GE	Genève	Av. d'Aïre	1945	3	MHNG/CSCF
VD	Valeyres-sous-Mont	Vsous-Mont	1960		CSCF
VD	Bogis-Bossey	Bogis-Bossey	1966	3	MHNG/CSCF
VD	Bellerive		1974		NMBE/CSCF
VD	Cudrefin		1976		CSCF
VD	Noville	Les Glariers	1985	3	CSCF
VD	Noville	Gros Brasset	1988	3	CSCF
FR	Gletterens	Gletterens	1957		CSCF
FR	Bas-Vully	Vully	1980		NMBE/CSCF
FR	Font	Vers L'Eglise	1980		CSCF
FR	Cheyres	Cheyres	1981	1	CSCF
FR	Galmiz	Le Chablais	?	3	MHNF
NE	Cressier		1966, 1970	1, 2	MHNG/CSCF
JU	Bonfol	Bonfol	1960	2	CSCF
BS	Basel	Bäumlihof-Hörnli	1909		NMBA/CSCF
BS	Basel	Lange Erlen	1940	2	CSCF
BS	Basel	Rheinhafen	1950		NMBA/CSCF
BS	Riehen	Eisweiher	1980		CSCF
BL	Allschwil	Herzogenmatt	1980		CSCF
BL	Bottmingen	Bruderholzhof	1980		CSCF
SO	Rodersdorf	Rodersdorf	1990	1	CSCF

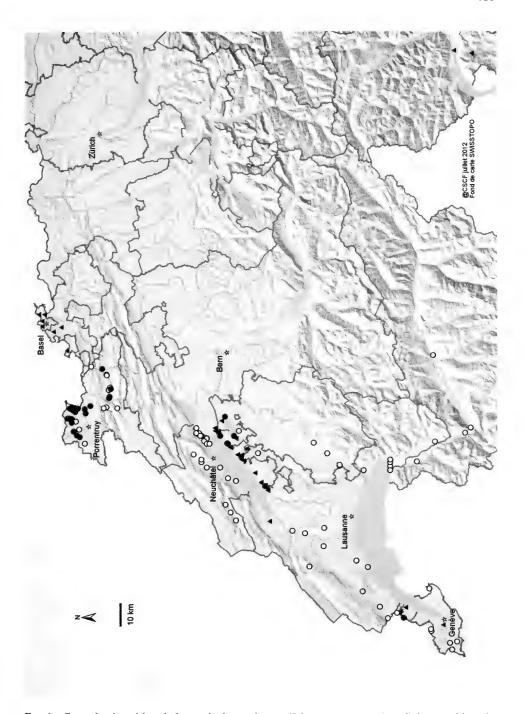


Fig. 1 - Carte de répartition de la souris des moissons (*Micromys minutus*) en Suisse occidentale. Triangles noirs: base de données du CSCF, observations anciennes, avant 2002 (tableau 1). Ronds noirs: observations nouvelles, après 2002. Ronds blancs: sites prospectés sans observations.

TABLEAU 2. Sites prospectés en Suisse occidentale dès 2005, hors de la Grande Cariçaie, avec présence constatée de *Micromys minutus*. La date mentionnée (avec n = nombre de nids correspondants) est la dernière observation réalisée pour chaque site, certains ayant été suivis sur plusieurs années.

Ct	Commune	Lieu-dit	Date	n	Altitu	de Coord X	Coord Y
		Marais du Grand-					
VD	Commugny	Bataillard	13.09.2010	24	468	500100	132780
VD	Salavaux	Petit Lac	13.10.2011	16	431	569050	196800
FR	Galmiz	Le Chablais	24.11.2010	1	431	576300	200180
JU	Damphreux	Les Coeudres	31.08.2007	28	440	575400	258000
JU	Damphreux	En Prâtchi	31.08.2007	1	430	575600	258875
JU	Bonfol	Etangs de Bonfol	23.10.2008	7	440	579800	257750
JU	Bonfol	Etangs Rougeat	23.10.2008	1	445	579350	256950
JU	Bonfol	Queue de Chat	23.10.2008	8	445	579400	258700
JU	Vendlincourt	Etang	23.10.2008	2	450	579350	255700
JU	Alle	Pisciculture	22.10.2008	6	455	577500	252700
JU	Cornol	Pré Raisin	22.10.2008	1	530	580350	250900
JU	Miécourt	Allaine	22.10.2008	2	470	579150	253100
JU	Boécourt	Les Esserts	24.10.2008	5	490	583850	243700
JU	Courfaivre	Les Aingles	24.10.2008	1	465	586750	243250
JU	Delémont	Le Colliard	29.10.2010	1	420	594350	246500
JU	Boécourt	Etang Bourquard	22.10.2009	1	497	583350	243900
JU	Bure	Le Teurion	30.10.2009	6	575	568550	254950
JU	Courtemaîche	Tcherteau	30.10.2009	1	545	569150	256050
JU	Courtemaîche	Etang	06.11.2009	2	390	570650	257300
JU	Lugnez	La Vouèvre	06.11.2009	1	430	575600	259550
JU	Vendlincourt	Combe aux Chiens	06.11.2009	1	445	578000	256700

Détails par cantons

Canton de Genève: En octobre 2007, 6 sites ont été prospectés dans le canton de Genève. Aucun indice de présence n'a été retrouvé dans ces derniers. Ainsi, une observation de nid au Moulin-de-Vert, faite par un garde de l'environnement il y a une quinzaine d'années, n'a pas pu être confirmée. Ces différents sites se situent entre 350 et 470 m d'altitude et d'une superficie variant de 2 à 7 ha. Ils sont composés de mosaïques de milieux humides, ne présentant que de petites surfaces de cariçaie et phragmitaies-cariçaies.

La présence de nids et d'une mâchoire dans une pelote de réjection est signalée par un observateur (J. Bordon) à l'Etournel (Ain, France) à moins d'un kilomètre de la frontière cantonale (G. Dändliker, comm. pers.). Les autres observations les plus proches le long du Rhône apparaissent dans le Marais de Lavours, situé à une quarantaine de kilomètres au sud du canton de Genève (J. Gilliéron, comm. pers.).

CANTON DE VAUD: En octobre 2007, quatre nids typiques de la souris des moissons ont été retrouvés dans le marais du Grand Bataillard (commune de Commugny, VD). Cette observation confirme la présence encore actuelle de cette espèce mise en évidence en 1966 déjà dans ce site par la collecte de trois nids par V. Aellen et P. Strinati (commune de Bogis-Bossey, VD), puis par l'observation d'un individu faite il y a une quinzaine d'année (S. Sachot, comm. pers.).

En juin 2008, une série de pièges et tunnels à traces ont été déposés à différents endroits dans ce marais et ses abords pour tester d'autres méthodes de détection de

cette espèce discrète. Aucune souris des moissons n'a cependant été capturée et aucune observation de traces ou de nids n'a été faite à ce moment là (Marchesi & Descombes, 2008). Afin de confirmer les premières observations réalisées en 2007, un nouveau transect au travers du marais a été effectué en octobre 2008: 39 nids typiques de la souris des moissons, plus ou moins frais ou en construction, ont pu être observés principalement dans un milieu composé d'une cariçaie à *Carex acutiformis* et parfois d'un mélange de cariçaie avec du *Phalaris*. En moyenne, les nids se situaient à 76 cm de hauteur (n= 39; min= 40 cm, max=100 cm).

En septembre 2010, un nouveau transect a permis de trouver 24 nids en parcourant une surface représentant environ la moitié du bas-marais. De vastes surfaces sont malheureusement de plus en plus colonisées uniformément par le solidage (*Solidago canadensis*), rendant le milieu stérile à toute autre espèce végétale, et non propice à la souris des moissons (Marchesi & Blant, 2010).

Au cours de l'automne 2010, des prospections effectuées dans 20 autres sites marécageux du canton de Vaud (hors Grande Cariçaie) n'ont permis de découvrir qu'un seul nouveau site avec des indices d'occupation sûrs de ce rongeur: la roselière de Salavaux située à l'extrémité Ouest du lac de Morat (Petit Lac, embouchure de la Broye). Quatre nids y ont été observés sur une petite bande très étroite entre forêt riveraine et roselière lacustre, en rive gauche de la Broye. Pas moins de 16 nids ont pu y être comptabilisés encore en 2011, tandis qu'un seul autre nid a pu être trouvé de l'autre côté de la Broye, en rive droite de l'embouchure. Dans le marais de Chavornay (Creux de Terre), un seul nid tressé a été trouvé dans la roselière-cariçaie malgré de longues fouilles. Une nouvelle recherche infructueuse effectuée en 2011 nous incite à penser que le nid trouvé en 2010 était celui d'un muscardin (nid tressé non attaché au support).

Les différentes recherches effectuées aux Grangettes entre 2002 et 2010 n'ont pas permis de mettre en évidence la souris des moissons malgré la recherche de nid et des essais de piégeage effectués en collaboration avec Peter Vogel de l'Université de Lausanne. Bien qu'une grande surface de milieux favorables ait été prospectée, les seuls nids trouvés ont été attribués au muscardin, aucun n'ayant les caractéristiques du tressage sur plante vivante effectué par *Micromys*. En 2002, un muscardin hibernait d'ailleurs dans un nid reposant sur une branchette de saule. Aucune souris des moissons n'a jamais été découverte lors des entretiens du site (O. Epars, comm. pers.).

Les sites vaudois occupés se situent à moins de 500 m d'altitude et semblent se répartir actuellement en deux sous-populations: la première située dans le Nord vaudois inféodée au bassin du Rhin, la deuxième représentée par la population du Grand Bataillard, dernier site connu actuellement pour cette espèce dans le bassin du Rhône suisse. Aucune observation n'a été faite entre ces deux sous-populations, dans la région des collines du Gros de Vaud. Le contact aurait pourtant pu se faire historiquement au niveau de la Sarraz, le seul point bas situé à moins de 500 m d'altitude.

CANTON DE FRIBOURG: Un site a été visité dans le canton de Fribourg, sur les bords du lac de Morat où l'espèce nous avait été signalée par André Fasel, directeur du Musée d'histoire naturelle de Fribourg (Marchesi & Blant, 2010). Comme dans la Grande Cariçaie, il existe sur la rive Est du lac une bande de cariçaie plus ou moins

large, entre la forêt riveraine et la roselière lacustre. Cette bande est plus étroite que sur la rive sud du lac de Neuchâtel, mais apparaît cependant très favorable. Un seul nid a été trouvé lors du contrôle, l'essentiel du milieu ayant déjà été fauché.

Deux autres sites visités en Gruyère (région de Semsales-Vaulruz, à plus de 800 m d'altitude) à l'occasion de piégeages se sont révélés négatifs, aucun nid de souris des moissons n'ayant pu être trouvé malgré la présence de surfaces de cariçaie jugées favorables dans des marais en bordure de plans d'eau.

CANTON DE NEUCHÂTEL: Sur 19 sites prospectés, aucun n'a été trouvé colonisé par la souris des moissons (Blant & Marchesi, 2009). Ces sites étaient situés entre 430 et 780 m d'altitude. L'étendue des cariçaies et phragmitaies-cariçaies (les cariçaies pures sont rares dans le canton de Neuchâtel) était comprise entre plusieurs hectares (rives lacustres) et 3 ares (surfaces résiduelles le long de canaux dans le Val-de-Ruz).

Le site ancien de Cressier est aujourd'hui occupé par une raffinerie de pétrole. Dans l'enceinte même de l'usine et à sa périphérie (réserve naturelle de la Vieille-Thielle) subsistent des milieux de phragmitaie-cariçaie résiduels de petite taille. Aucun indice de l'espèce n'a pu y être décelé. Une importante population y vivait pourtant dans les années 1960 (A. Meylan, comm. pers.). Les dernières données en ces lieux provenaient d'animaux découverts lors de la construction de la raffinerie, mise en service en 1966. La population s'était alors réfugiée sur des tas de terre dégrappée (A. Meylan, comm. pers.), au moins jusqu'en 1970. Les souris des moissons ont subsisté encore quelque temps dans ce site (feu A. Schertenleib, comm. pers.) sans qu'il soit possible de déterminer précisément le moment de leur disparition.

CANTON DU VALAIS: Aucun nid n'a été trouvé dans les rares milieux humides valaisans présentant quelques surfaces d'habitats potentiellement favorables (cariçaies et roselières peu denses). Cette espèce n'a d'ailleurs jamais été signalée dans ce canton.

Canton du Jura: Sur 29 sites visités, 17 étaient colonisés par la souris des moissons, avec des populations plus ou moins importantes (entre 1 et 28 nids recensés). Ces sites étaient situés entre 390 et 575 m d'altitude, en Ajoie et dans la Vallée de Delémont (Blant, 2007). L'étendue des cariçaies abritant l'espèce peut être de plusieurs hectares (Etangs de Damphreux), mais aussi de moins de 10 ares (ancienne pisciculture d'Alle, bassin de décantation de Tcherteau à Courtemaîche). Les sites non occupés étaient situés entre 400 et 610 m d'altitude. On trouve dans cette catégorie des objets présentant une surface de cariçaie à priori favorable de plusieurs hectares comme l'étang A16 des Montoies (Courfaivre). Réalisée il y a une quinzaine d'année, cette zone humide pourrait être encore trop récente pour abriter l'espèce, qui semble peu mobile. Aucun des quatre sites de compensation A16 entièrement nouveaux n'a d'ailleurs été colonisé par l'espèce.

La découverte d'un crâne dans une pelote de réjection d'effraie dans une région proche de la place d'armes de Bure nous a incités à visiter les quelques zones humides de ce secteur karstique de la Haute Ajoie. L'espèce colonise deux bassins de décantation dans le périmètre d'exercices militaires. Ces bassins sont transformés en basmarais à *Typha latifolia*. La souris des moissons s'y reproduit malgré une faible couverture en *Carex* sp.



Fig. 2. Une surface de cariçaie en bordure d'un étang à Damphreux, milieu typique de la souris des moissons (photo M. Blant).



Fig. 3. Une surface de bas-marais en bordure de la place d'armes de Bure, milieu secondaire avec *Typha* et graminées (*Agrostis gigantea*) (photo M. Blant).

RÉGION BÂLOISE: Deux sites ont été contrôlés dans cette région, pour tenter de retrouver la souris des moissons, dont la présence ancienne était connue (Fig. 1). Ces deux sites (cantons de Bâle-campagne et Soleure) se sont révélés positifs, avec au moins un nid. Au Herzogenmatt (Allschwil BL), il s'agit d'une population introduite dans un site revitalisé, alors qu'à Rodersdorf (SO) sa présence est probablement naturelle.

DISCUSSION

Typologie des milieux colonisés et non colonisés

La cariçaie (Magnocaricion) des bordures d'étangs de faible profondeur (avec en particulier Carex acutiformis) ou des rives de lacs et de cours d'eau lents constitue le milieu le plus colonisé par la souris des moissons, parmi les sites visités. Cependant, l'espèce peut occuper également parfois des phragmitaies avec Carex sp. (rives de l'Allaine, rive du lac de Morat), des bas-marais à Typha latifolia (place d'armes de Bure) ou des phalaridaies à Carex le long des cours d'eau, comme au Grand Bataillard. Böhme (1978) cite comme milieux primaires les associations à Calamagrostis, Typha et Carex. La colonisation des phragmitaies peut être limitée par le diamètre des tiges des vieux roseaux (Rahm, 1995), souvent trop épais pour les petites pattes du rongeur. Sa présence dans les cultures céréalières serait remarquée surtout dans le nord et l'ouest de l'Europe, en particulier en Grande-Bretagne. En Italie, elle fréquente surtout les rizières comme milieu humide de substitution. Sa présence dans d'autres milieux tels les jeunes pépinières est encore mentionnée dans la littérature (Moore et al., 2003).

Une des conditions nécessaires à la colonisation est la hauteur atteinte par les tiges de *Carex*, le tressage des nids débutant lorsque la végétation atteint environ 1,5 m selon les observations faites à Damphreux (Berret & Goetschi, 2009). De cette manière, tressés à mi-hauteur des tiges, les nids sont suffisamment élevés au-dessus du sol. Ils se situent aussi le plus souvent au-dessus d'un terrain inondable, au moins saisonnièrement. A l'inverse, les roselières terrestres et les cariçaies résiduelles trop sèches, avec une hauteur de végétation limitée (< 50 cm), ou encore les marais à petits *Carex* (Parvocariçaie) n'abritent pas l'espèce.

En l'absence de *Carex*, le nid peut être tressé avec des tiges de graminées, comme dans le *Phalaridion (Phalaris arundinacea)* ou les bas-marais à *Typha* (avec *Agrostris gigantea*). C'est le cas sur certaines surfaces du Grand Bataillard, ainsi qu'à Bure et au Herzogenmatt.

Les colonies de souris des moissons occupent des milieux de taille diverse, de plusieurs hectares à seulement quelques ares. Les surfaces de cariçaie colonisées peuvent même être encore plus petites. Dans ce cas, elles font généralement partie ou sont en contact avec des zones humides plus vastes. Par exemple, une surface de 10 m² à Bonfol (JU) contenait un nid, au bord d'un étang aux rives dégagées et distant de plus de 800 m d'autres surfaces de cariçaie favorable abritant d'autres nids. Aux Esserts à Boécourt (JU), une surface de moins de 100 m² contenait 11 nids de souris des moissons (Schmidlin, 2011) ! Toutefois, il est clair que les colonies occupant de grandes surfaces peuvent être plus importantes et ont donc plus de chance de subsister à long terme dans un paysage fragmenté.



Fig. 4. Nid de souris des moissons (Micromys minutus) (photo M. Blant).



Fig. 5. Le Grand Bataillard (VD) en novembre 2010, avec la surface fauchée à gauche et la bande préservée en lisière à droite qui reste favorable pour la construction des nids l'année suivante (photo P. Marchesi).

Dans le canton de Neuchâtel, la phragmitaie-cariçaie de la rive nord du lac n'est apparemment pas occupée par l'espèce. Elle n'est constituée tantôt que d'une bande mince de *Carex pseudocyperus*, tantôt plus large (jusqu'à 10-15 m) en retrait de la roselière lacustre. Le substrat minéral (galets) ne laisse cependant se développer que des tiges peu élevées, d'environ 1 m (par exemple La Ramée à Marin). Les quelques zones à végétation plus haute (1,5 à 2 m) sont rares (par exemple port de Bevaix).

Dans le canton de Genève, la plupart des sites actuels potentiellement favorables à la souris des moissons sont des milieux humides revitalisés, qui étaient souvent recouverts auparavant par la forêt. Un retour naturel de cette espèce dans ces basmarais est lié à un entretien adéquat favorisant les surfaces de cariçaie non boisées.

Urbanisation et fragmentation comme cause de l'absence

La disparition de la colonie de souris des moissons de l'Entre-deux-Lacs dans le canton de Neuchâtel a fait suite à la construction de la raffinerie de Cressier. L'industrialisation croissante et les modifications agricoles structurales (remaniements, drainages) ont limité ensuite les possibilités d'existence de l'espèce, qui semble devoir être considérée maintenant comme disparue de la région. Les quelques surfaces de *Carex* à longues tiges, subsistant en pied de berges de canaux de la Vieille Thielle ou d'un exutoire des drainages de la raffinerie sont de surfaces probablement trop modestes pour abriter encore l'espèce (au plus 20 à 30 m²).

Plusieurs sites visités se trouvent actuellement isolés par les surfaces cultivées et construites, ou sont déconnectés du réseau hydrographique, formant souvent les dernières liaisons biologiques entre les zones humides. Ceci fait suite au développement agricole et urbain et à la mise en tuyau, dans le passé, de tronçons de cours d'eau. C'est le cas par exemple de la petite zone humide de Dozière à Delémont, des anciennes rives du lac de Neuchâtel près de la jonction A5 à Auvernier-Colombier ou encore de la zone humide de Belmont, à Boudry. Ces sites n'abritent pas ou plus la souris des moissons. Cependant, la présence de l'espèce sur la place d'armes de Bure, à plus de 1,5 km du réseau hydrographique représenté par l'Allaine, laisse envisager une possibilité pour elle de se maintenir ou de coloniser des sites refuges à des distances proches des zones réservoirs, ceci même sans corridor offrant des milieux humides relais.

Isolement géographique et altitude

L'absence de colonies dans le Val-de-Ruz malgré la présence de milieux humides de surface assez importante (p. ex. La Paulière) pourrait être due à une cause purement géographique. Les gorges du Seyon situées au bas de la vallée constituent un verrou assez serré et peu propice au transit d'une petite espèce de milieu plutôt ouvert. L'absence dans le Val-de-Travers est due probablement au même type de barrière topographique (gorges de l'Areuse). L'absence de l'espèce aux Grangettes peut s'expliquer de manière similaire. Le delta du Rhône s'est transformé progressivement en milieu palustre à la fin du retrait des glaciers, mais cette région est cependant restée plus ou moins isolée du Plateau suisse pour certaines espèces par le lac ainsi que par les versants escarpés et boisés des Préalpes qui tombent abruptement dans le lac au niveau du Haut Léman (Riviera suisse, Chablais français). Plusieurs espèces de

batraciens comme le crapaud accoucheur (*Alytes obstetricans*) ou le crapaud calamite (*Bufo calamita*) n'ont de même probablement pas pu franchir ces obstacles pour se répandre dans la haute vallée du Rhône située en amont du Léman (Marchesi, obs. pers.).

L'altitude elle-même est probablement aussi un facteur limitant dans la distribution de l'espèce, expliquant son absence dans le Gros de Vaud, les vallées neuchâteloises ou les Préalpes fribourgeoises. Les observations faites en Suisse se situent en effet toutes à moins de 600 m d'altitude, la station la plus basse se situant à 310 m (Herzogenmatt, Allschwil BL), et la plus haute à 575 m (Le Teurion, Bure JU). En France voisine, Michelat *et al.* (2005) signalent la présence de ce petit rongeur jusqu'à près de 1000 m à Mouthe (Doubs, France), d'après des pelotes de réjection et une capture à la Tourbière des Pontets. Il n'est toutefois pas clairement établi que ce site NATURA 2000 abrite une population reproductrice de souris des moissons. Quéré et Louarn (2011) mentionnent en effet que cette espèce dépasse rarement 500 m d'altitude en France. L'existence d'une population viable à 1000 m d'altitude mériterait d'être authentifiée par une preuve de reproduction.

Importance respective des populations dans le contexte suisse

Les données du Groupe d'étude et de gestion (GEG) confirment une population de souris des moissons occupant de vastes surfaces de la Grande Cariçaie, sur la rive sud du lac de Neuchâtel. Il s'agit assurément de la population la plus importante en nombre de cette espèce pour la Suisse. Toutefois, le long des transects de comptage, des fluctuations annuelles du nombre de nids sont constatées (A. Gander, comm. pers.). Il est possible que la fauche des roselières ait une influence négative momentanée sur ce petit rongeur. Nous avons aussi remarqué au Grand Bataillard que les surfaces fauchées ne conviennent pas l'année suivante car elles ne présentent pas encore de roseaux ou de *Carex* de hauteur suffisante pour la construction des nids.

L'Ajoie dans le canton du Jura apparaît comme étant la seconde région possédant une population importante de cette espèce en Suisse. Répartie dans un vaste réseau de sites abritant des colonies plus ou moins nombreuses, elle est en relation avec celle du bassin sud-est de la France (Franche-Comté, Alsace du Sud), très riche en étangs et cours d'eau. En 1982-83, une analyse de pelotes de réjection faisait mention d'un nombre relativement important de crânes (68 exemplaires sur 6384) de souris des moissons dans les proies de l'effraie des clochers (Buser, 1984). Il apparaît donc que ce rongeur s'est bien maintenu dans cette région durant les 30 dernières années.

Trois autres populations certifiées récemment en Suisse se situent dans le bassin du Rhin: Lac de Morat, Vallée de Delémont, Bâle. Elles sont plus isolées et numériquement plus faibles. En ce qui concerne le bassin rhodanien, seuls les marais de la Versoix (Grand Bataillard) abritent encore une population numériquement importante, qui était certainement à l'époque en relation avec d'autres sites de la vallée du Rhône français, bien qu'aucune trace récente n'ait été trouvée entre deux à Genève.

Au Tessin, la souris des moissons a vraisemblablement disparu récemment du dernier site connu dans le Mendrisiotto, aucune trace n'ayant pu être retrouvée dans des cariçaies résiduelles (Blant *et al.*, 2005 ; T. Maddalena, comm. pers.). Cette extinction

locale est sans aucun doute due aussi à l'urbanisation et à l'implantation de zones industrielles, tout comme dans l'Entre-deux-Lacs neuchâtelois.

Eléments pour une gestion des milieux favorable à l'espèce

Dans la Grande Cariçaie, l'espèce est retenue comme prioritaire dans les plans de gestion avec comme objectif de suivi l'amélioration des exigences écologiques et de la distribution des espèces de priorité 1 (GEG, 2007). Ce leitmotiv devrait être appliqué à tous les autres sites abritant encore cette espèce très menacée en Suisse, en particulier les réserves naturelles occupées par des populations prospères (Marais de Damphreux, Grand Bataillard, Les Esserts/Boécourt). Cependant, de nombreux autres sites de plus faible dimension abritent encore l'espèce, mais sont menacés à plus ou moins court terme d'assèchement et/ou d'afforestation. Il est urgent de revitaliser le milieu humide de certains de ces sites, de manière à renforcer la cariçaie. C'est le cas par exemple à Salavaux, vers l'embouchure de la Broye, ou aux Aingles à Courfaivre dans la vallée de Delémont.

Les recommandations suivantes sont proposées pour la conservation de l'espèce:

- 1) Inventorier précisément l'espèce et ses besoins en habitat dans chaque site occupé (surface utilisée, densité et localisation des nids, type d'habitat), et assurer un monitoring annuel prenant en compte les effets de gestion et d'entretien des milieux.
- 2) Prévoir une fauche alternée sur un rythme d'au moins 3 ans dans les marais concernés, et laisser des bandes en friche, moins souvent entretenues, en lisière, au bord des bouquets de buissons et, si besoin, une bande non fauchée de 2-3 m de large à travers les grandes surfaces dénudées comme liaison entre les milieux favorables.
- 3) Effectuer la fauche de préférence d'octobre à mars pour ne pas porter atteinte aux nids occupés et à l'habitat estival. Eviter de faucher les touradons, car ils servent souvent de refuge à ce rongeur.
- 4) Laisser dans les lisières et autres surfaces moins intéressantes du marais des tas de branchages et de litière, ou des andins de roseaux comme refuge. Cette mesure probablement primordiale pour améliorer la survie hivernale de l'espèce est également utile à beaucoup d'autres animaux.
- 5) Suivant les sites, effectuer des interventions de débroussaillage partiel, utiles pour conserver l'habitat marécageux. Cependant, elles doivent tenir compte du fait que ce rongeur se réfugie souvent dans les boisements clairs et les lisières en hiver. Ces travaux se feront donc de manière fine et ponctuelle, et autant que possible sans grosses machines qui écrasent le sol ou les tas de branchages. Par divers aménagements, les castors peuvent être incités à contribuer naturellement à ce travail d'éclaircie.
- 6) Creuser des petites mares et fossés ou dégrapper des dépressions humides dans les grandes cariçaies monotones pour raviver la magnocariçaie et favoriser le développement de tiges élevées. Cela permettrait également de diversifier les milieux et offrir un spectre plus large de nourriture durant les saisons (graines, insectes).
- 7) Lutter contre l'envahissement par le solidage et les autres néophytes dans les sites protégés.

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Civizelotes new genus, and other new or little known Zelotinae (Araneae, Gnaphosidae)

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Civizelotes new genus, and other new or little known Zelotinae (Araneae, Gnaphosidae). - Civizelotes, a new genus of gnaphosid spiders, is established and divided in four species groups. Notes are given on the mating mechanisms of C. medianus (Denis) in the C. civicus-group. First descriptions are given of the male of Z. argoliensis (C. L. Koch, 1839), of the female of Drassyllus villicoides (Giltay, 1932) comb. n., the female of Civizelotes dentatidens (Simon, 1914) comb. n., the female of C. medianus (Denis, 1935) comb. n. C. medianoides sp. n., C. ibericus sp. n., and Heser hispanus sp. n. Transferred to different genera are: C. civicus (Simon, 1878) comb. n., C. caucasius (L. Koch, 1866) comb. n., C. solstitialis (Levy, 1998) comb. n., Heser nilicola (O. P.-Cambridge, 1874) comb. n., H. schmitzi (Kulczynski, 1899) comb. n., H. bernardi (Marinaro, 1967) comb. n., H. bonneti (Marinaro, 1967) comb. n., and H. incisupalpis (Levy, 1998) comb. n. Zelotes balcanicus Deltshev, 2006 is removed from the synonymy of Z. argoliensis.

Keywords: Arachnida - taxonomy - zoogeography - mating mechanism.

INTRODUCTION

A detailed study of the structure of the 3 pedipalp in Zelotes requires some generic transfers. In Zelotes str. s. the basic structure of the palp is: Strong posterior sclerite of terminal apophysis linked to posterior tegular base, radix or embolus (Fig. 1) and Senglet (2011: figs 13-14, 133). Massive embolar radix with a solid junction to the embolus (Fig. 2). The intercalary sclerite represents an extension of the basal sector of the embolar base, giving a ventral mobile joint to a terminal apophysis with a posterior fixation. All species with a different palp morphology need to be transferred to other genera. Among these species a monophyletic group is here recognised and separated into the new genus Civizelotes gen. n.

MATERIAL AND METHODS

Except for the \mathcal{P} syntypes of *Zelotes argoliensis* and the syntype of *Z. medianus* (Denis) = *Civizelotes dentatidens*, all material was collected by myself. Measurements are in millimetres. Vulvae were examined in lactic acid on an excavated microscopic slide. Holotypes and paratypes of the species described in here are deposited in the Natural History Museum of Geneva (MHNG); the other material, if not indicated

otherwise, remains in my private collection. For details on rearing and cryo-fixing of mated spiders see Senglet (2004: 87).

The typical leg spination according to Platnick & Shadab (1983) is: Femora; I, II d110, p001; III, IV d110, p011, r011; patella III r010; tibiae: III p111, v222, r011; IV p111, v222, r111; metatarsi: I, II v200; III p122, v221, r112; IV p122, v220, r122. Only differences from this pattern are given in the text. AME, ALE, PME, PLE and MOQ refer to anterior median, anterior lateral, posterior median, posterior lateral eyes and to the median ocular quadrangle (with eyes included).

Terminology of genital structures follows Senglet (2004: 88-90) and Senglet (2011: 514).

TAXONOMY AND FAUNISTIC DATA

Genus Zelotes Gistel, 1848

TYPE SPECIES: Melanophora subterranea C. L. Koch 1833, subsequent designation.

Zelotes fulvopilosus-subgroup of Z. thorelli-group (Senglet, 2011: 540)

Zelotes argoliensis (C. L. Koch, 1839)

Figs 3-10

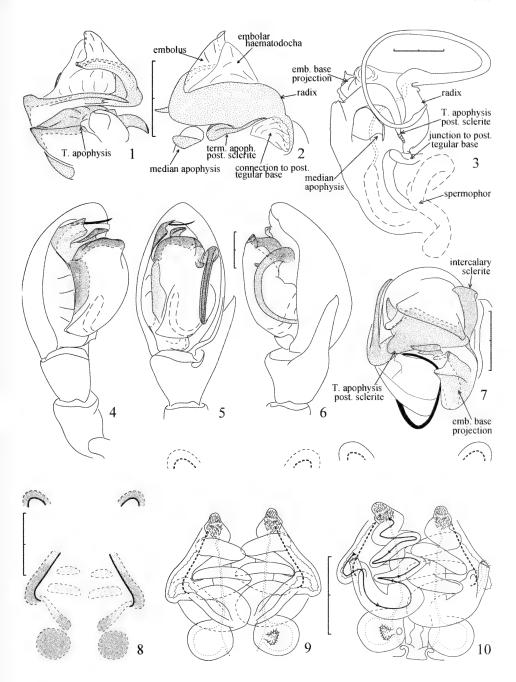
Melanophora argoliensis C. L. Koch, 1839: 72, fig. 483 (description of $\,$ $\,$). – L. Koch, 1866: 174, pl.7, fig. 113 ($\,$).

TYPE MATERIAL: BM1915.3.5.5759, Coll. Koch, Natural History Museum (London); 2 \$\,\text{syntypes from Greece}; received on loan through the courtesy of Mrs Janet Beccaloni.

OTHER MATERIAL EXAMINED: GREECE, Peloponnesus, Arcadia, Mt Mainalos, refuge, stones, 37°39'N 22°16'E; 2 $\stackrel{?}{\circ}$, 7 $\stackrel{?}{\circ}$ (last moults of $\stackrel{?}{\circ}$ 20.07 and 22.08, of 2 $\stackrel{?}{\circ}$ 26.08 and 07.09.2011); 25.05.2011.

DESCRIPTION: Large dark species. Prosoma dark brown, with black bristles. Opisthosoma black, covered with greyish adpressed hairs and black bristles. Legs dark brown; tarsi feebly lightened. Posterior eye row straight to slightly recurved

- ♂: Total length 5.20. Prosoma: 2.25 long, 1.85 wide, 0.90 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.06, ALE 0.12, PME 0.07, PLE 0.12; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.04, PME-PLE 0.07, ALE-PLE 0.07. MOQ length 0.26, front width 0.40, back width 0.42. Clypeus: 0.10 from AME, 0.08 from ALE. Pedipalp (Figs 3-7): Retrolateral tibial apophysis 2 times dorsal length of tibia. Patella dorsally longer than tibia. Tibia wider than long. Embolar base without connection to embolus, carrying a conical apical projection attached to embolar haematodocha, and a prolateral guide to embolus. Small hook of median apophysis half concealed by embolus. Very large, one-turn-coiled embolus reaching below proximal quarter of tegulum length. Posterior sclerite of terminal apophysis attached to base of embolar radix (Fig. 3), the latter linked through an intermediary junction to posterior tegular base. Tarsi I, II scopulate, metatarsi I, II only in apical 2/3. Leg spination: Tibiae III, r112; metatarsi III, VI v221. Scutum occupying 1/3 of opisthosoma length.
- ♀: Total length 6.26. Prosoma: 2.5 long, 2.00 wide, 1.08 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.07, ALE 0.12, PME 0.07, PLE 0.07; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.04, PME-PLE 0.04, ALE-PLE 0.07. MOQ length 0.24, front width 0.36, back width 0.46. Clypeus: 0.10 from AME, 0.08



Figs 1-10

(1-2) Zelotes apricorum (L. Koch), left male palp, cymbium removed. (1) Ventral view. (2) Dorsal view. (3-10) Z. argoliensis (C. L. Koch). (3-7) Left male palp. (3) Cleared, retrolateral view. (4) Prolateral view. (5) Ventral view. (6) Retrolateral view. (7) Cymbium removed, apical view. (8) Epigynum. (9) Vulva, ventral view. (10) Id., dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

from ALE. Epigynum (Fig. 8). Vulva (Figs 9-10): Copulatory duct loosely coiled around the straight median duct. Tarsi and metatarsi I and II entirely scopulate. Leg spination: Tibiae III, r011; metatarsi II, v220; III, VI v221.

Zelotes petrensis-group (Senglet, 2004: 94, 111)

Zelotes balcanicus Deltshev, 2006, removed from the synonymy of

Figs 11-12

Z. argoliensis Zelotes balcanicus Deltshev, in Deltshev et al., 2006: 711, figs 2-11 (description of ♂ and ♀). Zelotes baram Levy, 2009: 31, figs 67-70 (description of δ and \mathfrak{P}) syn. n.

Zelotes argoliensis. - Chatzaki, 2010: 54, figs 25-30 (\$\varphi\$, synonymy of Z. balcanicus) (misiden tification).

MATERIAL EXAMINED: GREECE, Macedonia, Thessaloniki, Loutra Apollonias, litter, 40°39'N 23°24'E; 1 ♀; 09.09.2004. – South of Stanos /Arnaia, *Pinus* litter, 40°32'N 23°35'E; 1 ♂, 1 ♀; 09.09.2004. – Epiros, Thesprotia, Arghyrotopos, litter, 39°25'N 20°19'E; 1 ♂ (last moult 05.09.2004); 31.08.2004. - Sterea Hellas, Phthiotidas, south-west of Theologos, Pinus litter, 38°39'N 23°11'E; 2 ♀ (last moults 07. and 18.09.2011); 17.06.2011. – Peloponnesus, Messenia, Kiparissia, leaf litter, 37°15′N 21°40′E; 1 ♀; 03.06.2011. – Laconia, East of Lira, Pinus litter, 36°39'N 22°58'E; 1 ♂, 1 ♀ (with palpus in microvial); 03.10.2004. – Argolida, above Platani, 700 m, 37°48'N 22°30'E; 3 \eth , 3 \diamondsuit (last moults of \eth 22.08.-02.09, of \heartsuit 02.08.-22.09.2011); 21.05.2011.

DESCRIPTION: See Deltshev et al. (2006: 711).

REMARKS: Contrary to its original placement in the Z. subterraneus-group, Z. balcanicus is a member of the Z. petrensis-group (Senglet, 2004: 94, 111), as can be seen from the structure of the embolar base. A strong mesal apophysis and a posterior sickle-shaped lamina on the embolar base (Figs 11-12) are present. A week direct sinuous link to the embolus is another basic character of the group. Lateral additional pockets are present on the epigynum. The absence of a membranous or sclerotized embolar projection is an indication that this species belongs to a distinct sub-group.

Genus *Drassyllus* Chamberlin, 1922

TYPE SPECIES: Drassyllus fallens Chamberlin, 1922, original designation.

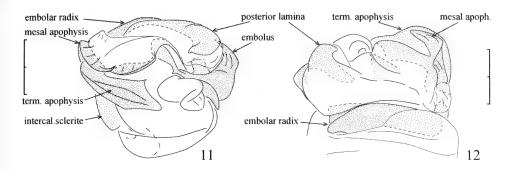
Drassyllus villicoides (Giltay, 1932) comb. n.

Figs 13-19

Zelotes villicoides Giltay, 1932: 28, fig. 18 (description of δ). – Giltay, 1933: 6, pl. 3, fig. 4 (δ). MATERIAL EXAMINED: GREECE, Macedonia, Thessaloniki, east of Chortiatis, stones in pasture, 40°37′N 23°07′E; 1 ♂ (last moult 02.06.2005); 07.09.2004. – West of Aghios Vassilios, 40°40′N 23°05′E; 1 ♂, 2 ♀ (last moults of ♂ 16.06.2005, of ♀ 08 and 14.05.2005); 08.09.2004. — Aghios Vassilios, 40°40′N 23°07′E; 1 ♀; 13.05.1968. — Loutra Apollonias, litter, 40°39′N 23°24'E; $1 \, \stackrel{?}{\circ}$, $1 \, \stackrel{?}{\circ}$ (last moults of $\stackrel{?}{\circ}$ 23.05.2005, of $\stackrel{?}{\circ}$ 09.07.2005); 09.09.2004. — Sterea Hellas, Phthiotidas, west of Malesina, 38°37'N 23°13'E; 6 ♂, 4 ♀ (last moults of ♂ 16.04.-15.05.2005, of ♀ 16.04.-28.05.2005); 25.09.2004. – Near Malesina, 38°37'N 23°13'E; 1 ♀; 21.05.1998. – Peloponnesus, Laconia, south-west of Mavrovouni, litter on sand, 36°43'N 22°32'E; 1 9; 26.05.2011. – Argolida, east of Ligourion, Lentiscus litter, 37°38'N 23°04'E, 1 ♂, 3 ♀ (last moults of 324.04.2005, of 917.04.24.05.2005; 01.10.2004.

DESCRIPTION: Prosoma dark brown, with tiny hairs. Opisthosoma black, with short adpressed hairs. Legs dark brown except for tawny-yellow tarsi and metatarsi. Tarsi and metatarsi I, II scopulate. Average size about 3/4 that of *D. praeficus*.

♂: Total length 5.00. Prosoma: 1.95 long, 1.62 wide, 0.77 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.07, ALE 0.08, PME 0.08, PLE 0.07;



Figs 11-12

Zelotes balcanicus Deltshev. (11) Left male palp, cymbium removed, anterior-apical view. (12) Id., dorsal view. Scale 0.2 mm.

AME-AME 0.03, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.04, ALE-PLE 0.06. MOQ length 0.20, front width 0.37, back width 0.43. Clypeus: 0.11 from AME, 0.07 from ALE. Retrolateral tibial apophysis bent dorsally, shorter than dorsal length of tibia. Pedipalp (Figs 13-16): Tibia short; its dorsal length about equal to lateral width. Patella dorsally longer than tibia. Scutum occupying 1/3 of opisthosoma length. Close to *D. praeficus*, differing by the thin narrow triangular terminal apophysis and the slender embolar radix apophysis (Figs 14, 16); in *D. praeficus* (Fig. 20) the latter is stronger and more cone-shaped.

\$\text{\$\congrue{2}\$: Total length 5.66. Prosoma: 2.10 long, 1.58 wide, 0.80 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.07, ALE 0.10, PME 0.08, PLE 0.08; AME-AME 0.08, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.05, ALE-PLE 0.05. MOQ length 0.24, front width 0.37, back width 0.43. Clypeus: 0.11 from AME, 0.06 from ALE. Epigynum and vulva (Figs 17-19). Anterior anchoring pockets at a distance from the anterior epigynal margins; in *D. praeficus* (Fig. 21) pocket pressed to the external margin of the epigynum. Modest widening of the lateral fold; median fold reaching the spermatheque in median-anterior position, there covered by cuticle (Figs 18-19); in *D. praeficus* (Fig. 21) posterior strong widening of the lateral fold; median fold reaching the spermatheque in uncovered lateral-anterior position.

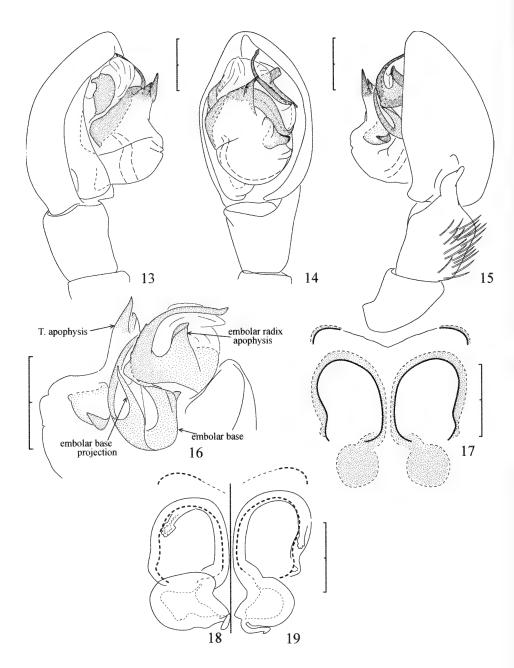
BIOLOGY: Adult males can be collected from April to June.

Drassyllus praeficus (L. Koch, 1866)

Figs 20-21

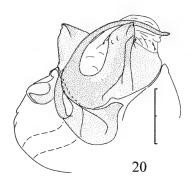
Melanophora praeficus L. Koch, 1866: 155, pl. 6, figs 97-99 (description of \eth and \Im). For previous synonymy see Platnick (2012).

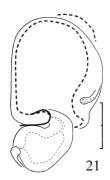
Material examined: SWITZERLAND, Vaud, Vich /Nyon; 1 & , 1 &; 01.-30.05.1996. — SPAIN: Lac de Sanabria, 42°06'N 06°41'W and 42°07'N 06°44'W; 1 &; 26.08.1971. — Avila, Road to parking Gredos /Hoyo del Espino, 1470 m, 40°18'N 05°12'W; 1 & (last moult 28.12.2009); 18.06.2009. — Andalusia, Granada, Prado de Zangarrilla (S. Nevada), stones, pasture, 2000 m., 37°07'N 03°26'W; 1 &; 29.05.2002. — FRANCE, Provence / Cote d'Azur, Var, Montauroux; 1 &; 07.06.1971. — Languedoc, Pyrénées Orientales, Prats de Mollo, 700 m., 42°24'N 02°25'E; 3 &; 29.06.2001. — Latour de Carol, 42°28'N 01°53'E; 1 &; 06.07.2001. — Above Mas Franco / Enveigt, 42°30'N 01°53'E; 1 &; 06.07.2001. — ANDORRA, La Rabassa, 2000 m, 42°26'N 01°32'E; 2 & (last moult of 1 & 24.02.2002); 08.07.2001. — West of St Julià



Figs 13-19

Drassyllus villicoides (Giltay). (13-16) Left male palp. (13) Prolateral view. (14) Ventral view. (15) Retrolateral view. (16) Cymbium discarded, retrolateral view. (17) Epigynum. (18-19) Two vulvae, dorsal view, same population.





Figs 20-21

D. praeficus. (20) Left male palp, cymbium removed, retrolateral view. (21) Left side of vulva, ventral view. Bold lines indicate epigynal folds. Scale 0.2 mm.

de Loria, schist litter, $42^{\circ}27'N\ 01^{\circ}28'E; 3 \$ (last moults of $2 \$ $9 \$ o5 and $9 \$ 05.2004); 27.05.2004. - GREECE, Macedonia, Serres, above Oreini, 1200 m, stones, 41°14′N 23°35′E; 1 ♀; 30.06.2011. – Thessaloniki, west of Aghios Vassilios, 40°40'N 23°05'E; 1 ♂, 1 ♀ (last moults of ♂ 11.06, of ♀ 09.06.2005); 08.09.2004. – Same; 4 ♀; 31.05.2008. – East of Aghios Vassilios, litter, 40°40'N 23°07'E; 2 & (last moults 17 and 20.06.2005); 08.09.2004. – Same; 2 &, 4 \(\circ\); 13.05.1968. - Same; 1 ♀; 28.05.1982. - Same, 40°40'N 23°07'E; 4 ♀; 14.06.1998. -Thessaloniki, 40°43'N 22°58'E; 1 ♀; 13.-18.05.1968. – Kastoria, north of Kastoria (pass), 40°35′N 21°18′E; 1 ♀; 20.06.1998. – Peloponnesus, Achaia, Kato Alissos, 38°09′N 21°35′E; 3 ♀ (last moult of 1 ♀ 10.05.1998); 29.04.1998. – Arla, 38°04'N 21°36'E; 1 ♀ (last moult of ♀ 05.05.1998); 30.04.1998. – Argolida, east of Myli / Nauplie, leaf litter, 37°35′N 22°44′E; 1 ♀ (last moult 03.06.2005); 01.10.2004. - Cyclades, Paros, Sta Maria /Naoussa, (Salicornia), 37°08'N 25°17'E; 1 ♀; 02.06.1998. – Crete, Chania, Omalos haut plateau, stones, 35°20'N 23°53′E; 2 ♂, 2 ♀ (last moults of ♂ 01.01 and 04.01, of ♀ 31.12.1999); 07.10.1999. – Episkopi, litter, soil crevices, 35°30'N 23°46'E; 1 ♀ (last moult 14.01.2000); 10.10.1999. – Rethimnon, Koxare /Spili, irigated vegetation, 35°14'N 24°28'E; 1 ♂, 2 ♀ (last moults of ♂ 30.12.1999, of 08.01.2000); 03.10.1999. - Choumerion / Pérama, 35°21'N 24°44'E; 1 ♂ (last moult 04.01.2000); 05.10.1999. – Missiria /Rethimnon, leaf litter, soil crevices, 35°22'N 24°31'E; 2 &; 06.10.1999. - Lassithi, Kato Metochi Lassithiou, 35°11'N 25°26'E; 2 ♂, 2 ♀ (with palpus in microvial, last moults of 3 25 and 30.12.1999, of 9 01.01 and 06.01.2000); 25.09.1999. – ROMANIA, Dobrogea, Constanca, Baneasa; 1 ♂ (with palpus in microvial); 30.05.1972. – Adamclisi; 1 δ ; 31.05.1972. – Mangalia; 2 \circ ; 02.06.1972. – Techirghiol; 1 \circ ; 03.06.1972. – BULGARIA, Razgrad, Hlebarovo; 1 ♀; 08.07.1972. – Varna, Slatni Pjasaci; 1 ♀; 11.07.1972. – Burgas, Obzor; 3 ♀; 14.07.1972. – Karnobat; 2 ♀; 15.07.1972. – Plovdiv, Backovo; 1 ♀; 21.07.1972. – IRAN, Esfahan, Lorestan, Dizgarán, 33°44′N 46°59′E; 3 ♀; 16.05.1974. – Fars, near Ghaderábád, 30°22'N 53°18'E; 1 ♀; 11.06.1974. – Khorasan, east of Chaman Bid, 37°26'N 56°37'E; 1 ♀; 14.07.1974.

DESCRIPTION: See Grimm (1985: 267, figs. 317, 319-320).

Drassyllus lutetianus (L. Koch, 1866)

Melanophora lutetianus L. Koch, 1866: 157, pl. 6, fig. 100 (description of \mathcal{P}). For previous synonymy see Platnick (2012).

MATERIAL EXAMINED: GREECE, Peloponnesus, Argolida, East of Myli /Nauplie, leaf litter, 37°35'N 22°44'E; 2 $\,$ (last moults 09 and 29.05.2005); 01.10.2004. – FRANCE, Corse, Sud Corse, Solenzara: 1 $\,$; 24.05.1971. – ITALIA, Sardinia, Sassari, Platamona / Porto Torres, damp leaf litter; 2 $\,$; 25.05.1999. – Ozieri, damp vegetation; 2 $\,$; 28.05.1999. – ROMANIA,

Dobrogea, Tulcea, Badabag; 1 $\,^\circ$; 05.06.1972. – Murighiol; 1 $\,^\circ$; 06.06.1972. – Constança, Baneasa; 1 $\,^\circ$; 30.05.1972. – BULGARIA, Razgrad, Hlebarovo; 1 $\,^\circ$; 08.07.1972.

DESCRIPTION: See Grimm (1985: 264, figs 8b, 315, 325-326).

Drassyllus pusillus (C. L. Koch, 1833)

Melanophora pusillus C. L. Koch, 1833: 120, pl. 22. For previous synonymy see Platnick (2012).

MATERIAL EXAMINED: SWITZERLAND, Vaud, Vich /Nyon, $46^\circ26'N\ 06^\circ15'E; 1\ \ensuremath{\mathfrak{F}}\ (with palpus in microvial); 02.05.2004. — Vich /Nyon; 2\ \ensuremath{\mathfrak{F}}\ (with vulva in microvial); 01.05.1996. — GREECE, Macedonia, Serres, Mt Vrondos (Laïlia) 1780 m, stones, 41°16'N 23°36'E; 1\ \ensuremath{\mathfrak{F}}\ (29.06.2011. — SPAIN, Castilla / Leon, Avila, Parking Gredos / Hoyo del Espino, 1780 m, pasture) 40°16'N 05°14'W; 2\ \ensuremath{\mathfrak{F}}\ (18.06.2009. — Nueva Castilla / La Mancha, Cuenca, Santa Cruz de Moya, 39°57'N 01°13'W; 1\ \ensuremath{\mathfrak{F}}\ (24.06.1971. — Palomera / Cuenca, 40°04'N 02°03'W; 3\ \delta; 27.06.1971. — Andalusia, Granada, Puerto de la Ragua, 2000 m., 37°07'N 03°02'W; 1\ \ensuremath{\mathfrak{F}}\ (18.06.1971. — IRAN, Azerbaidjan, Eastern Azerbaidjan, West of Bostanábád, 1900 m, 37°55'N 46°42'E; 1\ \delta; 07.06.1975.$

DESCRIPTION: See Grimm (1985: 274, figs 316, 327-328).

Genus Civizelotes gen. n.

TYPE SPECIES: Prosthesima civica Simon, 1878, designated herewith.

ETYMOLOGY: The first four letters of the type species are added as a prefix to Zelotes.

DIAGNOSIS: Embolar radix originating from the posterior margin of the tegulum, terminating at level of embolus in a large plate of bowl (Figs 47, 53-54, 62). Intercalary sclerite absent. Terminal apophysis without posterior sclerite, or reduced. Long embolus type. Leg spination: Femora IV p001, r001; metatarsi II v220.

REMARKS: Zelotes apricorum (Figs 1-2) shows both the embolar radix and the posterior sclerite of the terminal apophysis in Zelotes str. s.

KEY TO THE CIVIZELOTES-GROUPS

Civizelotes civicus-group

DEFINITION: Light coloured spiders. Male palp: A terminal apophysis present but without posterior sclerite. Strongly developed transverse embolar base forming a

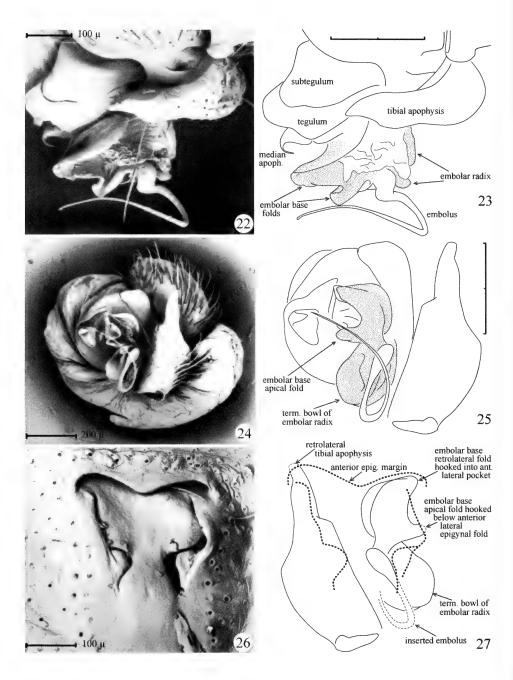
retrolateral loop (Figs 44, 47). Embolar radix visible prolaterally, with a large dorsal-apical bowl (Figs 31, 43). Epigynal plate narrowed in its centre (Figs 33, 35, 48). PME larger than PLE; posterior eye-row procurved; its eyes separated by less than 40% of their diameter. Of particular interest in this group is the use of the two folds of the embolar base to hold the bulbus on the epigynum (Figs 22, 26-27).

SPECIES INCLUDED: *C. civicus* (Simon, 1878) **comb. n.**, *C. medianus* (Denis, 1935) **comb. n.**, and *C. medianoides* sp. n.

MATING MECHANISM: *Civizelotes medianus* inserts the left pedipalp into the left side of the epigynum (Figs 22-29). The retrolateral tibial apophysis is inserted into the right anterior anchoring pocket. The erected embolar base (Figs 22-23) is forming two lobes, the apical and retrolateral folds. The wide retrolateral fold is inserted in the left anterior anchoring pocket of the epigynum, and the other below the left lateral epigynal fold (Figs 26-27).

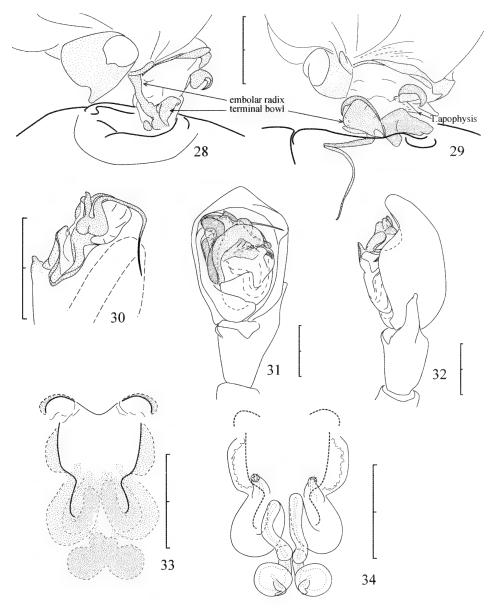
KEY T	O THE SPECIES OF THE <i>CIVIZELOTES CIVICUS</i> -GROUP			
ð				
9				
1a	Apical margin of embolar base with distal tooth (Figs 44, 47)			
1b	Apical margin of embolar base convex (Figs 31, 36)			
2a	Prolateral-apical part of embolar radix strongly developed (Fig. 31)			
2b	Prolateral-apical part of embolar radix feebly developed (Fig. 36) C. civicus			
3a	Lateral anterior epigynal folds straight, with a posterior bend (Figs 33, 48) 4			
3b	Anterior sector of epigynal folds curved, with visible median ducts			
	(Fig. 35)			
4a	Lateral anterior epigynal folds nearly parallel (Fig. 33) C. medianus			
4b	Lateral anterior epigynal folds diverging (Fig. 48) C. medianoides sp. n.			
Civize	Civizelotes medianus (Denis, 1935) comb. n. Figs 22-34			
- 1				

Zelotes medianus Denis, 1935: 118, figs 4-5 (description of \eth , not \Im , fig. 3=Z. dentatidens). – Jézéquel, 1962: 606, fig. 31 (\Im). – Soyer, 1967: 275, figs 5-7 (\Im may be the \Im of Z. dentatidens).



Figs 22-27

Civizelotes medianus (Denis), left male palp in copula. (22-23) Extracted male palp in anterior-lateral view. (24-25) Id., in apical view. (26) Epigynum, after extraction of palpal organ. (27) Id., palpal organ inserted. Bold lines indicate epigynal folds. Scale 0.2 mm.



Figs 28-34

Civizelotes medianus (Denis), (28-29) In copula. (28) Posterior view. (29) Lateral view. (30) Palpal organ, retrolateral view. (31) Left male palp, ventral view. (32) Id., retrolateral view. (33) Epigynum. (34) Vulva, dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

22.05.2002. — Sierra de Cazorla (Linarejas), 37°55'N 02°55'W; 1 δ ; 22.05.2002. — Cañada de las Hazadillas, Pinus, 37°39'N 03°43'W; 2 δ ; 30.05.2002. — Sevilla, east of Cazalla de la Sierra, deep leaf litter, 37°57'N 05°45'W; 2 δ , 3 \circ (last moult of 1 \circ 07.06.2009); 04.06.2009. — FRANCE, Languedoc, Aude, Bedos pass / Mouthoumet, 42°58'N 02°34'E; 2 \circ (last moult of 1 \circ 01.06.2004); 30.05.2004. — Eastern Pyrenees, Les Abeilles / Banyuls, 42°28'N 03°04'E;

1 ♂, 1 ♀; 28.06.2001. — Cerbère, stones in Cistus, 42°27'N 03°09'E; 3 ♂, 1 ♀ (last moult of 1 ♂ 05.06.2004); 22.05.2004. — ANDORRA, St Julià de Loria, oak litter, 42°27'N 01°29'E; 1 ♀ (last moult of ♀ 01.07.2004); 25.05.2004. — West of St Julià de Loria, litter, vegetation, 42°27'N 01°28'E; 3 ♂, 1 ♀ (last moult of ♀ 14.06.2004); 27.05.2004.

DESCRIPTION: Prosoma tawny, with short adpressed hair and sparse bristles. Opisthosoma blackish, with short adpressed hairs and short to medium-long bristles. Legs dark tawny to brownish. Leg spination: Femora IV p001, r001; metatarsi II V220. Tarsi I, II scopulate.

♂ from the same locality: Total length 4.12 (3.66). Prosoma: 1.80 (1.53) long, 1.40 (1.21) wide, 0.63 (0.58) wide at level of posterior eyes. Eye sizes and interdistances: AME 0.07, ALE 0.10, PME 0.07, PLE 0.09; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.03, ALE-PLE 0, 05. MOQ length 0.23, front width 0.33, back width 0.37. Clypeus: 0.07 from AME, 0.04 from ALE. Pedipalp (Figs 30-32): Retrolateral tibial apophysis shorter than tibial dorsal length. Patella dorsally longer than tibia. Superior margin of embolar base rounded in ventral view. Scutum occupying 1/4 of opisthosoma length.

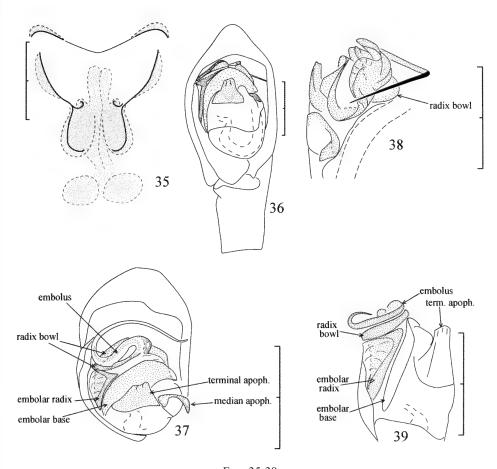
 $\$ \$\text{\$\text{?}}\$ from the same locality: Total length 4.90 (4.10). Prosoma: 1.92 (1.6) long, 1.48 (1.2) wide, 0.72 (0.64) wide at level of posterior eyes. Eye sizes and interdistances: AME 0.08, ALE 0.11, PME 0.11, PLE 0.08; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.03, ALE-PLE 0.04. MOQ length 0.17, front width 0.35, back width 0.38. Clypeus: 0.06 from AME, 0.08 from ALE. Epigynum and vulva (Figs 33-34). Anterior sector of epigynal folds diverging feebly, posterior sector shorter than in *Z. medianus*.

Civizelotes civicus (Simon, 1878) comb. n.

Figs 35-39

Prosthesima civica Simon, 1878: 80, pl. 14, fig. 20 (description of \eth and \Im). For previous synonymy see Platnick (2012).

MATERIAL EXAMINED: SPAIN, Catalonia, Barcelona, Alto de los Bruch, 41°36'N 01°45′E; 3 ♂; 13.06.1971. – Gelida, 41°27′N 01°51′E; 5 ♀; 14.06.1971. – Levant / Murcia, Valencia, Ayora, 39°03'N 01°03'W; 1 ♂; 20.06.1971. – Montroy, 39°20'N 00°35'W; 1 ♀; 22.06.1971. – Requena - Chera, 39°36'N 00°57'W and 39°32'N 01°00'W; 2 ♂, 1 ♀; 23.06.1971. – Alicante, Elda, 38°30'N 00°47'W; 2 ♀; 19.06.1971. – Murcia, Bullas, below vegetation, 38°02'N 01°39'W; 2 ♂; 18.05.2002. – Bullas, 38°02'N 01°39'W; 1 ♂, 5 ♀; 04.07.1971. – Caravaca, 38°05′N 01°52′W; 1 ♀; 05.07.1971. – Lac de Sanabria, 42°07′N 06°44′W and 42°06′N 06°41'W; 1 ♀; 26.08.1971. – Valladolid, Peñafiel, 41°35'N 04°08'W; 1 ♂, 1 ♀; 23.06.2002. – Salamanca, Puente Alagón /Sequeros, 40°30'N 05°57'W; 1 🗜; 13.08.1971. – Nueva Castilla / La Mancha, Madrid, Navalcarnero, 40°18'N 03°56'W; 1 ♂; 12.06.1969. – Aldea del Fresno (rio Alberche), 40°19'N 04°13'W; 1 ♂; 13.06.1969. – Cuenca, Santa Cruz de Moya, 39°57'N 01°13'W; 1 $\,^\circ$; 24.06.1971. – Palomera /Cuenca, 40°04'N 02°03'W; 1 $\,^\circ$; 27.06.1971. – Toledo, Escalona del Alberche, 40°10'N 04°24'W; 4 $\,^\circ$, 2 $\,^\circ$; 14.06.1969. – Urda /Consuegra, 39°25'N 03°42'W; 1 ♀; 12.08.1969. – Albacete, La Gineta (rio Jucar), fine leaf litter, 39°10'N 01°58'W; 1 ♂, 5 ♀ (last moults of 4 ♀ 20.-31.05.2002); 16.05.2002. – La Gineta (rio Júcar), 39°11'N 01°58'W; 2 ♀; 28.06.1971. – Hellin, 38°29'N 01°37'W; 1 ♀; 29.06.1971. – Ciudad Real, Ruidera, 38°56'N 02°51'W; 5 \, 9; 07.08.1969. — Ojos del Guadiana /Daimiel, 39°08'N 03°34'W; 1 ♀; 13.08.1969. – Estremadura, Caceres, Jarandilla (rio Tietar), 40°01'N 05°37'W; 3 ♂, 1 ♀; 16.06.1969. – Badajoz, south of Monesterio, stones in vegetation, 38°03'N 06°14'W; 3 &, 3 &; 05.06.2009. – South of Venta del Culebrin / Monesterio, 37°58'N 06°14'W; 1 ♀; 19.06.1969. -Rio Sillo (Higuera la Real), 38°06'N 06°41'W; 1 ♀; 14.06.2009. – Andalusia, Granada, Prado de Zangarrilla (S. Nevada), stones, pasture, 2000 m, 37°07′N 03°26′W; 3 ♂, 5 ♀ (last moults of ♀ 27.05.-02.06.2002); 29.05.2002. - Puebla de Don Fadrique, 1000-1200 m, 38°00'N 02°27'E; 2



Figs 35-39

Civizelotes civicus (Simon). (35) Epigynum. (36) Left male palp, ventral view. (37) Id., slightly expanded, ventral-apical view. (38) Id., cymbium discarded, retrolateral view. (39) Id., prolateral view. Bold lines indicate epigynal folds. Scale 0.2 mm.

♂, 6 ♀; 06.07.1971. – Pampaneira /Orgiva, 1200 m, 36°57'N 03°22'W; 2 ♀; 10.07.1971. – Caratauna /Orgiva, $36^{\circ}56^{\circ}N$ $03^{\circ}25^{\circ}W$; $1 \circlearrowleft$, $6 \circlearrowleft$ (with palpus in microvial); 13.07.1971.Capileira, 1500 m, 36°58'N 03°21'W; 1 δ , 8 \circ ; 10.07.1971. – Trevélez, 37°00'N 03°16'W; 1 \circ ; 14.07.1971. – Huéneja, 37°11'N 02°56'W; 1 ♂, 6 ♀; 16.07.1971. – Lacalahora (Ferreira), 37°10′N 03°03′W; 4 ♀; 17.07.1971. – Guadix (Paulenca de G.), 37°19′N 03°09′W; 6 ♀; 18.07.1971. – Jaen, Sierra de Cazorla (Fuente del Oso), 37°55′N 02°56′W; 5 ♂; 21.05.2002. – Sierra de Cazorla (Fuente del Oso), 37°55'N 02°56'W; 1 9; 23.07.1971. – Sierra de Cazorla (El Sagreo), 37°57'N 03°57'W; 1 ♀; 22.07.1971. – Sierra de Cazorla (Guadalquivir), 37°58'N $03^{\circ}55'W$; 2 \(\cong : 24.07.1971. — Cañada de las Hazadillas, Pinus, 37°39'N $03^{\circ}43'W$; 4 \(\delta , 1 \) \(\delta (last moult of ♀ 02.06.2002); 30.05.2002. – La Aliseda (Sierra de Andujar), 38°22'N 03°49'W; 2 ♂ (last moult of 1 ♂ 02.06.2009); 29.05.2009. – Hinojares / Cazorla, 37°43'N 02°59'W; 1 ♀; 19.07.1971. – Cordoba, Los Villares / Cordoba, Eucalyptus litter, 37°58'N 04°49'W; 3 \$, 5 \$ (last moults of 2 ♀ 12. and 19.06.2009); 31.05.2009. – Palma del Rio (Retortillo dam), leaf litter, 37°51'N 05°22'W; 1 ♂; 03.06.2009. – Malaga, Ronda, 36°46'N 05°13'W; 1 ♀; 21.07.1969. – Sevilla, La Minilla dam / El Ronquillo, 37°40'N 06°11'W; 2 \, 20.06.1969. – Alcala del Rio, 37°31'N 05°59'W; 1 \(\phi\); 22.06.1969. — Castilblanco (road C.433), 37°41'N 05°59'W; 1 \(\phi\);

23.06.1969. – El Real de la Jara - El Pintado, 37°57'N 06°03'W; 3 \$\,\circ\$; 03.07.1969. – Huelva, East of Aracena, 37°52'N 06°31'W; 1 \$\,\circ\$, 5 \$\,\circ\$; 07.06.2009. – Puerto Gil /Aracena, cork-oak leaf litter, 37°53'N 06°29'W; 1 \$\,\circ\$, 2 \$\,\circ\$; 07.06.2009. – Alajar /Aracena, 37°52'N 06°40'W; 2 \$\,\circ\$, 10 \$\,\circ\$ (with vulva in microvial); 07.07.1969. – Alajar 2 /Aracena, 37°53'N 06°40'W; 1 \$\,\circ\$, 1 \$\,\circ\$; 09.06.2009. – Fuenteheridos, deep leaf litter, 37°54'N 06°40'W; 2 \$\,\circ\$, 4 \$\,\circ\$; 12.06.2009. – Molino del rio Alajar, deep leaf litter, 37°52'N 06°40'W; 1 \$\,\circ\$; 13.06.2009. – Zalamea la Real, 37°41'N 06°39'W; 2 \$\,\circ\$; 10.07.1969. – PORTUGAL, Beira Alta, Guarda, Maceira / Fornos de Algodres, (Casal do Monte), 40°44'N 07°24'W; 1 \$\,\circ\$; 09.08.1971. – FRANCE, Provence / Cote d'Azur, Var, Cogolin; 2 \$\,\circ\$; 08.06.1971. – Languedoc, Eastern Pyrenees, Prats de Mollo, 700 m, 42°24'N 02°25'E; 1 \$\,\circ\$; 29.06.2001. – Arles sur Tech, 42°27'N 02°36'E; 1 \$\,\circ\$; 01.07.2001. – Latour de Carol, 42°28'N 01°53'E; 1 \$\,\circ\$; 06.07.2001. – ANDORRA, west of St Julià de Loria, 1400 m, schist litter, 42°27'N 01°28'E; 1 \$\,\circ\$; 08.07.2001. – Same; 2 \$\,\circ\$; 29.06.2002. – Same; 2 \$\,\circ\$, 2 \$\,\circ\$ (last moults of \$\,\circ\$ 31.05 and 27.06, of 1 \$\,\circ\$ 07.06.2004); 27.05.2004. – MOROCCO, Dayet Aaoua, 33°39'N 05°02'W; 1 \$\,\circ\$; 27.06.1967.

DESCRIPTION: See Grimm (1985: 80, pl. 14, Fig. 20).

Civizelotes medianoides sp. n.

Figs 40-49

HOLOTYPE: SPAIN, Andalusia, Cordoba, Alajar /Aracena, 37°52'N 06°41'W; \eth ; 07.06.2002.

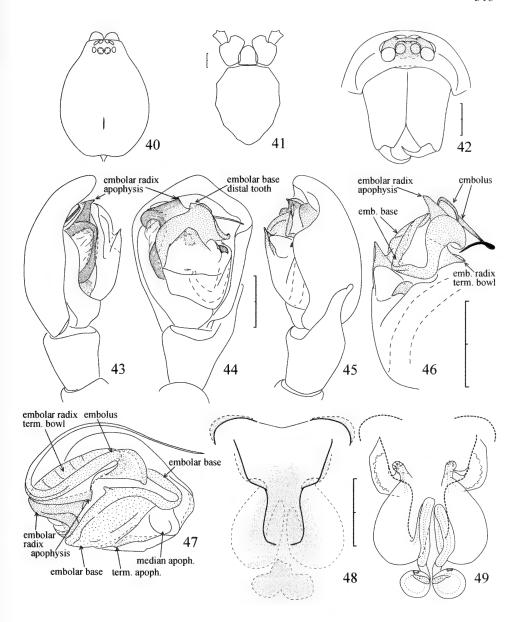
PARATYPES: Same locality as for holotype; 1 3, 1 4 (with vulva in microvial); 07.06.2002. — Alajar 1 /Aracena, cork oak leaf litter, 37°52'N 06°41'W; 5 3, 1 4 (last moult of 4 12.06.2009); 09.06.2009. — SPAIN, Andalusia, Cordoba, Breña dam, evergreen oaks litter, 37°51'N 05°04'W; 1 4 (last moult 10.06.2002); 01.06.2002. — Huelva, Linares de la Sierra /Aracena, 37°54'N 06°37'W; 1 4; 05.07.1969. — Same; 2 4; 05.06.2002. — Huelva, north of La Nava, schist litter, 38°00'N 06°45'W; 1 4, 1 4 (last moult of 4 10.08.2002); 09.06.2002.

Other Material examined: SPAIN, Cordoba, Alajar /Aracena, 37°52'N 06°40'W; 1 $\,^\circ$; 07.07.1969. – Puerto de Alajar, 820 m, evergreen oak leaf litter, 37°53'N 06°40'W; 3 $^\circ$, 1 $\,^\circ$ 9 (last moult of $\,^\circ$ 9 22.06.2009); 10.06.2009. – Molino del rio Alajar, deep leaf litter, 37°52'N 06°40'W; 1 $^\circ$ 5, 3 $\,^\circ$ 5; 13.06.2009. – Palma del Rio (Retortillo dam), leaf litter, 37°51'N 05°22'W; 1 $^\circ$ 5; 03.06.2009. – Road Posada-Villaviciosa 2, stones in Pinus litter, 37°00'N 05°05'W; 1 $\,^\circ$ 9; 02.06.2009. – Estremadura, Badajoz, Rio Sillo (Higuera la Real), 38°06'N 06°41'W; 2 $\,^\circ$ 9 (last moult of 1 $\,^\circ$ 9 16.06.2009); 14.06.2009.

ETYMOLOGY: The species name reflects the close relationship with $\it C.\ medianus$ (Denis).

DESCRIPTION: Prosoma and legs tawny. Opisthosoma grey, with darker hairs. Tarsi I, II scopulate. Leg spination: Femora IV p001, r001; metatarsi II v220.

- đ: Total length 4.50. Prosoma: 2.00 long, 1.50 wide, 0.69 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.08, ALE 0.10, PME 0.08, PLE 0.08; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.04, ALE-PLE 0.04. MOQ length 0.27, front width 0.36, back width 0.40. Clypeus: 0.08 from AME, 0.06 from ALE. Pedipalp (43-47): Patella and retrolateral tibial apophysis longer than dorsal length of tibia. In ventral view a small conical apophysis visible on superior ventral margin of embolar base. Scutum occupying 1/5 of opisthosoma length.
- $\$: Total length 4.75. Prosoma: 2.22 long, 1.58 wide, 0.81 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.08, ALE 011, PME 0.10, PLE 0.10; AME-AME 0.04, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.04, ALE-PLE 0.04. MOQ length 0.29, front width 0.40, back width 0.43. Clypeus: 0.08 from AME, 0.06 from ALE. Epigynum (Fig. 48): Median narrowing of lateral folds greater than in *C. medianus*. Vulva (Fig. 49).



Figs 40-49

Civizelotes medianoides sp. n., male. (40) Carapace. (41) Sternum. (42) Male chelicerae and ocular group, anterior view. (43) Left male palp, prolateral view. (44) Id., ventral view. (45) Id., retrolateral view. (46) Id., cymbium discarded, retrolateral view. (47) Id., apical view. (48) Epigynum. (49) Vulva, dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

Civizelotes dentatidens (Simon, 1914) comb. n.

Figs 50-57

Zelotes dentatidens Simon, 1914: 156, 217, fig. 293 (description of δ). Z. medianus Denis, 1935: 118, fig. 3 (description of δ , not figs 4-5 = Z. medianus). – Soyer, 1967: 275, figs 1-4 (not figs 5-7 = Z. medianus).

MATERIAL EXAMINED: Museum National d'Histoire Naturelle, Paris, 1 slide PM26 (syntype of *Z. medianus* Denis), 1 vulva. – SPAIN, Catalonia, Gerona, Cap de Creus, below rosemary, Cistus, Erica, 42°19'N 03°17'E; 1 \circlearrowleft (last moult 08.06.2004); 24.05.2004. – Estremadura, Caceres, Jarandilla (rio Tietar), 40°01'N 05°37'W; 1 \updownarrow ; 16.06.1969. – Andalusia, Granada, La Calahora, pine forest, 37°10'N 03°03'W; 2 \updownarrow (with 1/2 vulva in microvial); 23.05.2002.

DESCRIPTION of ♂: Femora, patellae and tibiae of legs blackish. Prosoma orange-yellow. Opisthosoma dorsally black, with black hairs, ventrally grey, with very short hairs. Leg spination: Femora IV p001, r001; metatarsi II v220. Total length 4.3. Prosoma 1.74 long, 1.33 wide, 0.61 wide at level of posterior eyes. Eye size and interdistances: AME 0.07, ALE 0.85, PME 0.10, PLE 0.08; AME-AME 0.04, AME-ALE, PME-PME 0.10, PME-PLE 0.10, ALE-PLE 0.02. MOQ length 0.24, front width 0.36, back width 0.36. Clypeus 0.08 from AME, 0.05 from ALE. Pedipalp (Figs 50-54): Terminal apophysis present. Embolar radix with a large dorsal-apical bowl (Fig. 54). Patella dorsally longer than tibia. Strong tibial apophysis with a tapering tip and a dorsal tooth. Retrolateral margin of cymbium strongly notched at level of embolus. Embolar base with a strong ventral branch terminating in a flattened, conical, retrolaterally directed tip. Embolus emerging from the strong short erected dorsal branch with a conical ventral apophysis. Terminal apophysis without posterior sclerite, straight, with the soft tegular cuticle reaching the second third of its length. Radix forming a large concave bowl at level of embolus (Figs 53-54). Scutum brown, occupying 1/3 of opisthosoma.

Description of $\,^\circ$: Prosoma and legs tawny. Opisthosoma dorsally grey, with darker hairs, ventrally tawny. Total length 4.25. Prosoma: 2.00 long, 1.43 wide, 0.78 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.09, ALE 0.11, PME 0.11, PLE 0.08; AME-AME 0.07, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.03, ALE-PLE 0.06. MOQ length 0.28, front width 0.40, back width 0.43. Clypeus: 0.11 from AME, 0.06 from ALE. Epigynum (Fig. 55) with scapus-like anterior anchoring pockets protruding ventrally. Vulva (Figs 56-57).

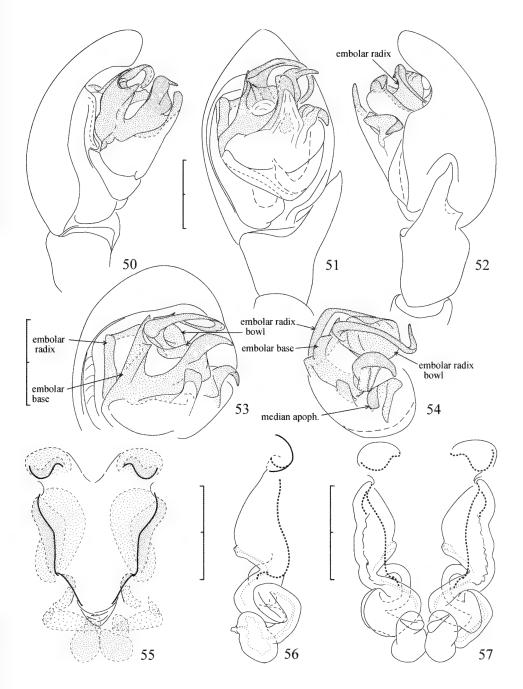
Civizelotes gracilis-group

I have not seen *C. gracilis* and *C. pygmaeus*, but the detailed drawings of Miller (1967) give good clues.

DEFINITION: 3 pedipalp: Embolus emerging from the terminal plate of the embolar radix ("scheibenförmige Basalplatte" in Miller (1967: 269) and "Truncus" in Miller (1967: pl. 4, figs 3-4, 7-8). Radix emitting a pointed apophysis near to the base of embolus (Figs 59, 62) and "S" in Miller, 1967: pl. 4, figs 3-4, 7-8).

Female: Epigynal plate in anterior sector (Fig. 66 and Grimm, 1985: figs 236, 238).

SPECIES INCLUDED: *C. gracilis* (Canestrini, 1968) **comb. n.**, *C. pygmaeus* (Miller, 1943) **comb. n.**, and *C. ibericus* **sp. n.**



Figs 50-57

Civizelotes dentatidens (Simon). (50-54) Left male palp. (50) Prolateral view. (51) Ventral view. (52) Retrolateral view. (53) Prolateral-ventral-apical view. (54) Ventral-apical view. (55) Epigynum. (56) Vulva, external-lateral view. (57) Id., dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

Civizelotes ibericus sp. n.

Figs 58-66

HOLOTYPE: SPAIN, Andalusia, Cordoba, Breña dam, evergreen oaks litter, 37°51'N 05°04'W; δ ; 01.06.2002.

Paratypes: SPAIN, Nueva Castilla / La Mancha, Toledo, Cardiel de los Montes (rio Alberche), 40°02'N 04°39'W; 1 $\,^{\circ}$ (with vulva in microvial); 15.06.1969. – Andalusia, Granada, Pradollano (S. Nevada), stones, dwarf Juniperus, 2350 m., 37°07'N 03°24 2 $\,^{\circ}$ (with vulva in microvial); 28.05.2002. – Huelva, Santa Olalla (rio Cala), 37°55'N 06°11'W; 1 $\,^{\circ}$; 04.07.1969.

ETYMOLOGY: The species name reflects the biogeography of the new species.

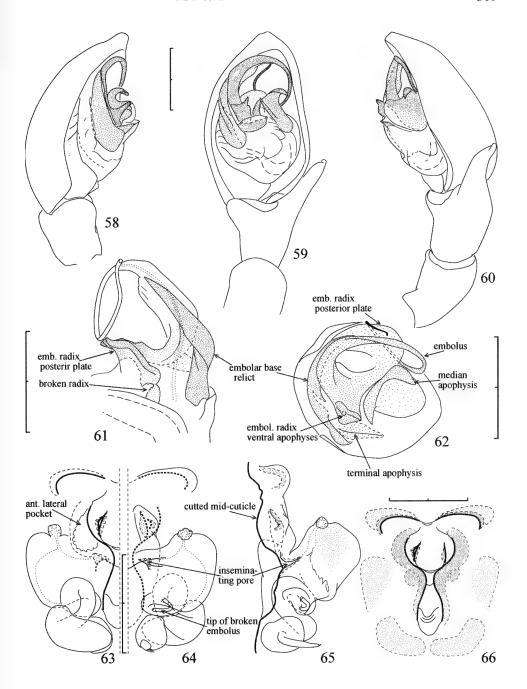
Description of 3: Prosoma tawny-brown, with a few posterior bristles. Opisthosoma grey, with medium-long hairs. Legs brown. Total length 4.00. Prosoma: 1.90 long, 1.43 wide, 0.80 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.06, ALE 0.08, PME 0.07, PLE 0.07; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.04, ALE-PLE 0.04. MOQ length 0.20, front width 0.34, back width 0.40. Clypeus: 0.08 from AME, 0.05 from ALE. Pedipalp (Figs 58-62): Patella longer than dorsal tibia length. Terminal plate of embolar radix expanded into a posterior branch catching the embolar loop (Fig. 62). Radix expanding into a membranous flap along the embolus (Fig. 61). Radix emitting a pointed apophysis at base of embolus. Relict embolar base less reduced than in *C. gracilis* and *C. pygmaeus*, coupled to a relict terminal apophysis. Strong median apophysis with a large elevated base. Leg spination: Femora III r001; IV p001, r001; metatarsi I v000, II v220. Tarsi I, II scopulate. Scutum occupying 1/4 of opisthosoma length.

Description of $\ \$: Prosoma dark brown. Opisthosoma black, with mediumlong hairs. Legs brown, with tarsi and metatarsi slightly lighter; old specimens much lighter. Total length 3.60. Prosoma: 1.46 long, 1.10 wide, 0.58 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.05, ALE 0.08, PME 0.07, PLE 0.07; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.03, ALE-PLE 0.04. MOQ length 0.19, front width 0.28, back width 0.31. Clypeus: 0.06 from AME, 0.03 from ALE. Epigynum with sinuous lateral folds (Fig. 66). Anterior median sector filled with a globular epigynal plate containing two slits; lateral pockets situated below the folds. Vulva (Figs 63-65). Leg spination: Femora IV p001, r001; metatarsi I, II v220. Tarsi I, II scopulate.

DIAGNOSIS: *Civizelotes ibericus* differs from the other two species in this group: 1 Absence of a prolateral tegular apophysis ["h" for "Höcker des Tegulum" in Miller (1967: pl. 4, figs 3-4, 7-8)]. 2 Embolar base less vestigial and presence of a relict terminal apophysis at its base. The female paratypes found in central and southern Spain are indicating a wide distribution in Spain, and the probability that they are conspecific with the male holotype is great.

Civizelotes caucasius-group

DEFINITION: Posterior eye row procurved. & pedipalp: Strong elongated embolar radix (Fig. 67) terminating in a bowl. Embolar base containing the sperm duct (Fig. 68), reaching straight to the radix bowl. Relict terminal apophysis with a posterior sclerite without distinct connection. Embolus long, curled right (clockwise) on left palp. Atrium in anterior epigynal sector.



Figs 58-66

Civizelotes ibericus n. sp. (58-62) Left male palp. (58) Prolateral view. (59) Ventral view. (60) Retrolateral view. (61) Cymbium removed, dorsal view. (62) Id., apical view. (63) Vulva, ventral view. (64) Id., dorsal view. (65) Id., median-lateral view. (66) Epigynum. Bold lines indicate epigynal folds. Scale 0.2 mm.

SPECIES INCLUDED: C. caucasius (L. Koch, 1866), C. sostitialis (Levy, 1998).

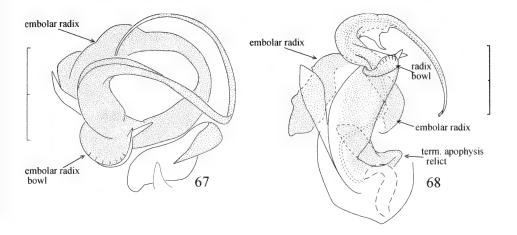
REMARKS: The structure of the pedipalp (Figs 65-66), with a long embolar radix and a developed embolar base, excludes these species from the *Civizelotes gracilis*-group. The study of copulatory mechanism (Senglet, 2004: 95, figs 26-31) shows that the embolar base and radix are penetrating to mid-length of the vulva; radix not figured, but radix bowl visible at base of embolus (Senglet, 2004: fig. 31).

Civizelotes caucasius (L. Koch, 1866) comb. n.

Figs 67-68

Melanophora caucasia L. Koch, 1866: 144, pl. 6, fig. 87 (description of \mathcal{P}). For previous synonymy see Platnick (2012).

MATERIAL EXAMINED: GREECE, Macedonia, Serres, above Oreini, 1200 m, stones, 41°14'N 23°35'E; 5 ♂, 3 ♀; 30.06.2011. – Thessaloniki, west of Aghios Vassilios, 40°41'N 23°05′E; 1 ♂ (last moult 17.06.2008); 31.05.2008. – Aghios Vassilios, 40°40′N 23°07′E; 2 ♀ (last moults of ♀ 29.07. and 02.08.1998); 14.06.1998. – East of Apollonia, below stones, $40^{\circ}37^{\circ}N$ 23°32′E; 7 ♂, 3 ♀ (last moults of ♀ 01.07.2008); 01.06.2008. – Loutra /Volvi lake, 40°39'N 23°25'E; 3 ♂ (last moults of 2 ♂ 16 and 22.06.1998); 14.06.1998. – Kastoria, north of Kastoria (pass), $40^{\circ}35'N\ 21^{\circ}18'E$; $5 \stackrel{?}{\circ}$, $3 \stackrel{?}{\circ}$ (last moults of $2 \stackrel{?}{\circ} 21$. and 25.06.1998); 20.06.1998. - Thessalia, Larissa, Gonnos, 39°51'N 22°28'E; 1 ♂; 19.05.1968. - Sterea Hellas, Phthiotidas, 2 ♀; 15.06.1968. – Same; 6 ♂, 3 ♀ (with vulva in microvial, last moults of ♂ 23.05.-25.06, of ♀ 02.-23.06.1998); 21.05.1998. – Mt Chlomos, 860 m, stones, 38°36'N 23°10'E; 2 ♂, 5 ♀ (last moults of 4 ♀ 16.06.-01.07.2011); 14.06.2011. – Same, 980 m, stones, 38°36'N 23°01'E; 3 ♂, 3 ♀ (last moults of ♀ 15.06.-01.07.2011); 14.06.2011. − Tràgana, 38°37'N 23°07'E; 1 ♀; 21.05.1968. – Glyphada / Theologos, 38°39'N 23°14'E; 1 ♀; 04.06.1978. – Theologos, 38°39'N 23°12′E; 3 ♂, 3 ♀ (with vulva in microvial, last moults of ♀ 29.05.-01.06.1998); 20.05.1998. – Eubea, Theologos, 38°29'N 23°47'E; 1 &; 11.06.2008. – Dystos lake, 38°22'N 24°08'E; 1 &; 17.06.1981. – Peloponnesus, Laconia, south-west of Monemyasie, stones, 36°40'N 23°01'E; 1 ♀ (last moults of ♂ 25.06.1998, of ♀ 01.09.1998); 13.05.1998. – Arcadia, east of Langadas, 830 m, stones, $37^{\circ}40'N$ 22°03'E; $3 \stackrel{?}{\circ}, 2 \stackrel{?}{\circ}$ (last moults of $\stackrel{?}{\circ}$ 09.-27.06, of $\stackrel{?}{\circ}$ 08 and 27.07.2011); 05.06.2011. – Argolida, Palaia Epidauros, Pinus litter, 37°39'N 23°09'E; 1 ♂; 01.10.2004. – Same 1 δ ; 05.06.1981. – Same; 2 δ , 2 \Im (last moults of 1 δ 17.05, of \Im 14.05 and 05.06.1998); 14.05.1998. – Above Platani, 700 m, 37°48'N 22°30'E; 4 $\stackrel{?}{\circ}$, 1 $\stackrel{?}{\circ}$ (last moults of $\stackrel{?}{\circ}$ 20.06.-01.07, of ♀ 15.07.2011); 21.05.2011. – Corinthos, east of Angelokastro, stones, 37°45'N 23°01'E; 1 ♀ (last moult of ♀ 07.07.2011); 24.05.2011. – Cyclades, Paros, Sta Maria /Naoussa, Salicornia, 37°08'N 25°17'E; 1 ♀; 02.06.1998. – Naxos, north-east of Sangri, 37°03'N 25°27'E; 1 ♀ (last moult of ♀ 18.06.1998); 05.06.1998. – North of Aghios Prokopios, dry, below stones, 37°05'N 25°21′E; 1 ♀; 06.06.1998. – Koronido, 650-750 m, 37°09′N 25°37′E; 5 ♀ (last moults 28.06.-03.07.1998); 08.06.1998. - Crete, Irakleion, Damasta; 1 ♀; 28.06.1970. - Chàrakas, Eucaliptus bark, 35°01'N 25°08'E; 1 ♂ (last moult 22.03.2000); 01.10.1999. – Lassithi, Kaminàkion; 1 ♂, 1 ♀; 13.07.1970. – SPAIN, Nueva Castilla / La Mancha, Albacete, La Gineta (rio Jucar), fine leaf litter, 39°10'N 01°58'W; 2 ♂ (last moults 10 and 16.07.2002); 16.05.2002. – Ciudad Real, Fuencaliente, 38°23'N 04°18'W; 3 \(\chi\); 03.08.1969. – Ruidera, 38°56'N 02°51'W; 1 \(\chi\); 07.08.1969. - Estremadura, Badajoz, south of Venta del Culebrin / Monesterio, 37°58'N 06°14'W; 1 ♂ (last moult 19.06.1969); 19.06.1969. – Andalusia, Granada, La Vidriera / Pto del Pinar, 38°03'N 02°34'W; 1 ♀ (last moult of ♀ 05.07.2002); 20.05.2002. – Road Puerto de la Ragua, pine forest, 37°09'N 03°03'W; 1 ♂ (last moult 10.07.2002); 24.05.2002. – Collado del Muerto (S. Nevada), 1450 m, 37°08′N 03°28′W; 2 ♂ (last moults 13 and 22.07.2002); 29.05.2002. – Cordoba, Almodóvar del Rio (Breña dam), 37°50'N 05°04'W; 1 ♂; 01.06.2009. – Sevilla, Pintado dam /Cazalla de la Sierra, 37°59'N 05°57'W; 1 ♂, 1 ♀; 02.07.1969. – Huelva, Santa Olalla (rio Cala), 37°55'N 06°11'W; 1 &; 04.07.1969. – PORTUGAL, Beira Alta, Guarda, Maceira / Fornos de Algodres (Casal do Monte), 40°44'N 07°24'W; 1 ♂; 09.08.1971. –



Figs 67-68

Civizelotes caucasius (L. Koch), left male palp, cleared. (67) Apical view. (68) Ventral-prolateral view.

BULGARIA, Centre, Pazardzik, Pestera; 1 $\,^\circ$; 23.07.1972. – IRAN, Caspian See, Mazanderan, near Dasht, 37°19'N 56°04'E; 1 $\,^\circ$; 27.07.1974.

DESCRIPTION: See Grimm (1985: 281, figs 231, 234-235).

Civizelotes solstitialis (Levy, 1998) comb. n.

Zelotes solstitialis Levy, 1998: 139, figs 97-101 (description of ♂ and ♀). – Chatzaki, Thaler & Mylonas, 2003: 60, figs 46-47, 50.-51. – Deltshev, Lazarov & Blagoev, 2004: 194, figs 12-14. – Seyyar, Demir & Topçu, 2006: 50, figs 2A-B (♂).

MATERIAL EXAMINED: GREECE, Sterea Hellas, Phthiotidas, Tràgana, 38°37'N 23°07'E; 1 $\$; 13.07.1968. — Theologos, 38°39'N 23°12'E; 2 $\$ 3, 1 $\$ 4 (last moults of $\$ 3 15. and 17.08, of $\$ 5 07.09.1998); 20.05.1998. — Cyclades, Naxos, Aria /Philoti, 37°02'N 25°29'E; 1 $\$ 5 (last moult 06.09.1998); 11.06.1998.

DESCRIPTION: See Levy (1998: 139, figs 231, 234-235).

REMARK: In *C. solstitialis* half of the radix bowl is concealed by the very large base of the embolus.

Genus *Heser* Tuneva, 2005

Type species: Heser malefactor Tuneva, 2005, original designation

REMARK: Tuneva characterized the genus largely by the lack of typical *Zelotes* organs. In *Zelotinae* the terminal apophysis is a ventral branch of the embolar base; in *Heser* this is not present. The embolar base is strongly reduced. The embolus arises from the prolateral sector. Females have no glandular ducts (blind paramedian ducts).

Heser nilicola-group

DEFINITION: In these species the apical part of the tegulum is grooved to support the embolus; in the type species the embolus rests on the prolateral part of the median apophysis. Apical grooved sector sometimes partly sclerotized. Long embolus curled

left (conter-clockwise) on the left palp. Palpal tibia and retrolateral apophysis short. Embolar base variably reduced. No intercalary sclerite present; the base of the embolar base (Figs 69, 77, 79) can be mistaken for a intercalary. Median apophysis large, except in *H. hispanus*. The glandular ducts (blind paramedian ducts) are replaced by scattered glands (Figs 75, 83, 89).

SPECIES INCLUDED: *Heser nilicola* (O. P.-Cambridge, 1874), *H. schmitzi* (Kulczynski, 1899), *H. incisupalpis* Levy, 1998, *H. bernardi* Marinaro, 1967, *H. bonneti* Marinaro, 1967 and *H. hispanus* sp. n.

KEY'	TO SPECIES OF THE HESER NILICOLA-GROUP
3	
9	3
1a	Median apophysis small (Figs 85-86)
1b	Median apophysis large (Figs 70, 77)
2a	Embolar base reduced; embolus arising from basal prolateral tegular
	sector (Figs 76, 79)
2b	Embolar base with a projection; embolus arising from dorsal tegular
	sector (Figs 71-72)
3a	Epigynal plate elongated or triangular (Figs 81-82, 87)
3b	Epigynal plate rounded (Figs 73-74)
4a	Epigynal plate triangular, widened almost to the anterior anchoring
	pockets width (Fig. 87)
4b	Epigynal plate with more or less parallel sides (Figs 81-82) H. schmitzi

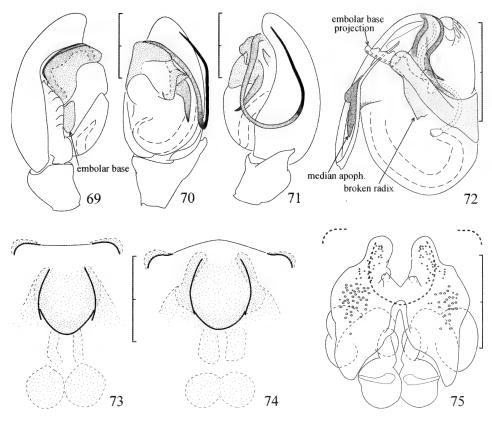
Heser nilicola (O. P.-Cambridge, 1874)

Figs 69-75

Prosthesima nilicola O. P.-Cambridge, 1874: 380, pl. 5, fig. 8 (description of ♂) For previous synomymy see Platnick (2012).

DESCRIPTION: See Platnick & Shadab (1983: 274, figs 316, 327-328).

REMARKS: The cleared δ palp shows a relatively well developed embolar base with a projection (Figs 69-72). The base of the embolar base may be mistaken for an intercalary sclerite. \mathfrak{P} : The epigynal plate is rounded. The distance between epigynal plate and anterior anchoring pockets is highly variable. Greek form (Fig. 73): Platnick & Shadab (1983: figs 265-266, showing a faulty connection of the median vulval duct); Chatzaki *et al.* (2003: fig. 85); FitzPatrick (2007: Fig. 95). Occidental form (Fig. 74,



Figs 69-75

Heser nilicola (O. P.-Cambridge). (69) Left male palp, prolateral view. (70) Id., ventral view. (71) Id., retrolateral view. (72) Id., cleared, dorsal view. (73) Epigynum, from Greece. (74) Id., from Sardinia. (75) Vulva, dorsal view (Sardinia). Bold lines indicate epigynal folds. Scale 0.2 mm.

Sardinia): Cornick *et al.* (2004: fig. 3a); Melic (1995: figs 1-2, showing a faulty connection of the median vulval ducts): Sardinia, Corsica, south of France and north Spain.

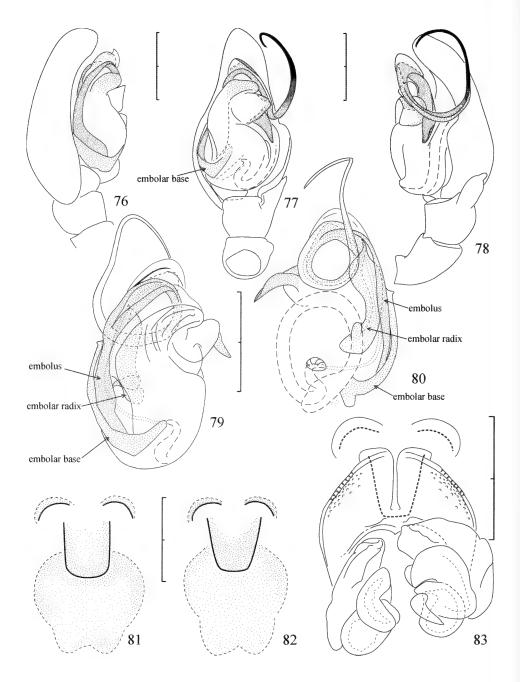
Heser schmitzi (Kulczynski, 1899)

Figs 76-83

Prosthesima schmitzii Kulczynski, 1899: 359, pl. 6, fig. 32 (description of ♀). *Zelotes schmitzi.* – Platnick & Murphy, 1998: 118, figs 1-4 (♀, description of ♂).

MATERIAL EXAMINED: SPAIN, Levant / Murcia, Alicante, Elche, palm grove, $38^{\circ}17'N$ $00^{\circ}42'W$; $1\ \footnote{3}$; 15.05.2002. — Elda, $38^{\circ}30'N$ $00^{\circ}47'W$; $1\ \footnote{3}$; 19.06.1971. — Murcia, Archena, $38^{\circ}07'N$ $01^{\circ}17'W$; $1\ \footnote{3}$; 17.05.2002. — Andalusia, Almeria, Adra (La Albufera), cultivated dryed pond, $36^{\circ}46'N$ $02^{\circ}58'W$; $10\ \footnote{3}$, $3\ \cite{3}$ (last moults of $2\ \footnote{3}$ 27.05 and 27.05 an

DESCRIPTION: Prosoma and legs brown, with lighter tarsi. Opisthosoma black, with adpressed hairs and black bristles. Leg spination: Femora IV r001; tibiae III r111, IV p110; metatarsi I v000, IV v220/222. Tarsi I, II scopulate.



Figs 76-83

Heser schmitzi (Kulczynski). (76-80) Left male palp. (76) Prolateral view. (77) Ventral view. (78) Retrolateral view. (79) Cleared, prolateral-ventral view. (80) Id., dorsal view. (81-82) Two epigyna, same population. (83) Vulva, dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

- ♂: Total length 3.05. Prosoma: 1.36 long, 1.03 wide, 0.54 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.04, ALE 0.07, PME 0.06, PLE 0.06; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.02, ALE-PLE 0.03. MOQ length 0.10, front width 0.16, back width 0.18. Clypeus: 0.06 from AME, 0.04 from ALE. Pedipalp (Figs 76-80): Patella dorsally longer than tibia. In cleared bulbus (Figs 79-80) a short embolar radix and a vestigial embolar base visible. Median apophysis large. Scutum occupying 40% of opisthosoma length.
- ♀: Total length 4.70. Prosoma: 1.53 long, 1.14 wide, 0.60 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.04, ALE 0.07, PME 0.06, PLE 0.06; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.04, PME-PLE 0.03, ALE-PLE. MOQ length 0.14, front width 0.27, back width 0.31. Clypeus: 0.04 from AME, 0.03 from ALE. Epigynum (Figs 81-82), epigynal plate variable, with sides parallel to feebly diverging. Vulva (Fig. 83) with scattered glands on the sides.

Heser hispanus sp. n.

Figs 84-89

HOLOTYPE: SPAIN, Estremadura, Badajoz, Monesterio, 38°05'N 06°16'W; \eth ; 19.06.1969.

Paratypes: Same locality as for holotype; 1 $\,^{\circ}$ (with vulva in microvial); 19.06.1969. – Spain, Andalusia, Sevilla, Alanis, 38°02'N 05°11'W; 2 $\,^{\circ}$ (with vulva in microvial); 01.07.1969.

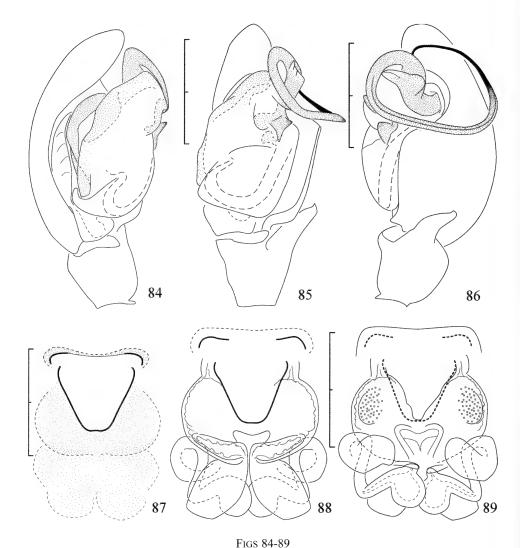
ETYMOLOGY: The species name refers to the geographical occurrence of these spiders.

DESCRIPTION ♂ HOLOTYPE: Prosoma mid-brown, with medium-sized bristles. Opisthosoma black, covered with medium-long bristles. Tarsi I, II scopulate. Total length 2.76. Prosoma: 1.20 long, 0.87 wide, 0.48 wide at level of posterior eyes. Eye sizes and interdistances: AME 0.03, ALE 0.07, PME 0.06, PLE 0.06; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.02, ALE-PLE 0.04. MOQ length 0.12, front width 0.20, back width 0.23. Clypeus: 0.06 from AME, 0.04 from ALE. Pedipalp (Figs 84-86): Patella dorsally longer than the short tibia. Retrolateral tibial apophysis shorter than tibia, dorsally arched. Embolus emerging from backside of tegulum. Median apophysis small. Scutum occupying 35% of opisthosoma length. Leg spination: Femora IV p001, r001; metatarsi I v000; II v210; III-IV v221.

DESCRIPTION ♀ FROM ALANIS: Prosoma tawny-brown, with median to long bristles. Opisthosoma blackish, covered with dense median light coloured bristles. Legs entirely tawny. Total length 3.40 (3.26). Prosoma: 1.24 (1.22) long, 0.93 wide, 0.48 wide at level of posterior eyes. Eye size and interdistances: AME 0.04, ALE 0.06, PME 0.042, PLE 0.042; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.03, PME-PLE 0.02, ALE-PLE 0.03. MOQ length 0.14, front width 0.20, back width 0.24. Clypeus: 0.04 from AME, 0.04 from ALE. Epigynum (Fig. 87) with triangular epigynal plate, its anterior part almost as wide as anterior anchoring pockets. Vulva (Figs 88-89 from Alanis) with scattered glands on the dorsal sides. Leg spination: Femora IV p001, r001; tibiae IV p110; metatarsi I v000; IV r112.

Heser infumatus (O. P.-Cambridge, 1872)

Drassus infumatus O. P.-Cambridge, 1872: 238, pl. 15, fig. 16 (description of \eth and \Im). *Heser infumatus*. Tuneva, 2005: 323 (transfer of \eth and \Im from *Zelotes*). For previous synomymy see Platnick (2012).



Heser hispanus sp. n. (84) Left male palp, prolateral view. (85) Id., ventral view. (86) Id., retrolateral view. (87) Epigynum. (88) Vulva, ventral view. (89) Id., dorsal view. Bold lines indicate epigynal folds. Scale 0.2 mm.

MATERIAL EXAMINED: GREECE, Cyclades, Paros, Parikia; 1 ♀; 25.06.1968.

DESCRIPTION: See Levy (1998: 145, figs 112-115).

REMARK: Not a member of the *Heser nilicola*-group; the female of *H. infumatus* has the anterior epigynal margin ventrally projected like a scapus.

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Leptopsalis foveolata sp. n., a new species of Stylocellidae from Thailand that displays a novel morphological feature in the suborder Cyphophthalmi (Arachnida, Opiliones)

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Leptopsalis foveolata sp. n., a new species of Stylocellidae from Thailand that displays a novel morphological feature in the suborder Cyphophthalmi (Arachnida, Opiliones). - Leptopsalis foveolata sp. n., a species of Southeast Asian mite harvestman with an exceptional morphology, is described. Males and females of this species bear rows of deep pits on the dorsal and ventral side of the posterior end of their body. These pits are strongly granular but do not bear obvious pores or especially dense concentrations of micropores. Also, many of the large granules on the body surface are flattened and digitated, and many around the pits are grooved. This is a new morphological feature in the suborder Cyphophthalmi, and its function is not clear. The species is only known from the type locality, Mt Sankalakheeree in Pattani Province, southern Thailand, formerly known as Bukit Besar.

Keywords: Taxonomy - mite harvestmen - opisthosomal pits - Namtok Sai Khao - Bukit Besar.

INTRODUCTION

Stylocellidae is a family of Cyphophthalmi that can be found from the Eastern Himalayas to New Guinea and out to the Philippines, and which likely arrived in Southeast Asia on the Sibumasu terrane that rifted from the northern Gondwanan coastline in the Paleozoic (Clouse & Giribet, 2010). Cyphophthalmi in general are small harvestmen that favor humid leaf litter and caves, and which, until recently, were poorly understood and not commonly collected. Now that their remarkably poor dispersal abilities have been shown to make them excellent models for vicariance biogeography (Boyer *et al.*, 2007; Giribet *et al.*, 2012), and as collecting techniques have improved, new collections of Cyphophthalmi have become more routine (Giribet, 2000). These collections have revealed considerable biodiversity, especially in tropical families (Benavides & Giribet, 2007; Clouse & Giribet, 2010). Moreover, not all of these new species differ by subtle body proportions (copulatory organs are still poorly

investigated); some present entirely new morphological features, as in the species we describe here.

Stylocellid taxonomy has recently been updated after the publication of several new phylogenetic hypotheses (Clouse *et al.*, 2009; Clouse & Giribet, 2010; Giribet *et al.*, 2012). Twenty-seven of the family's 34 described species had been placed in the genus *Stylocellus*, four in *Fangensis*, and the remaining three distributed one each in *Leptopsalis*, *Miopsalis* and *Meghalaya* (Clouse & Giribet, 2007; Giribet, 2000; Giribet *et al.*, 2007; Schwendinger & Giribet, 2005). *Leptopsalis beccarii* Thorell, 1882 (the type of that genus) was in the synonymy of *Stylocellus sumatranus* Westwood, 1874 (see Thorell, 1890) for about a century, but it has been resurrected (informally in Clouse *et al.*, 2009 and in Giribet, 2002; formally after examination of types in Clouse & Giribet, in press) and will soon receive fourteen species transferred from *Stylocellus* (Clouse, in press; Clouse & Giribet, in press). It is now understood that *Leptopsalis* encompasses the bulk of the family's undescribed diversity, including all species on Sulawesi, New Guinea and Java, as well as most species on Sumatra and the Thai-Malay peninsula (Clouse & Giribet, 2010). The species described here is the first to be originally assigned to *Leptopsalis* in 130 years.

The types of the new species were collected at Sai Khao Waterfall, at the foot of Mt Sankalakheeree (or Sankalakhierie) which peaks at ca 1000 m altitude. This is an isolated, still densely forested granite mountain massiv at the border of Pattani, Yala and Songkhla Province, known under the Malay names "Bukit Besar" (= big hill) and "Gunong Negiri" before the Sultanate of Pattani came under Siamese rule in 1909. Bukit Besar was sampled by the "Skeat-Expedition" in May 1899 (Skeat, 1954) and by the "Annandale & Robinson-Expedition" (N. Annandale took part in both expeditions) in April-May and August-September 1901 (Annandale & Robinson, 1903). The discovery of a velvet-worm (probably *Eoperipatus* sp.) on Bukit Besar during the "Skeat-Expedition" highlights the presence of typical Malayan faunal elements. Other such elements (of arachnids) await publication.

MATERIALS AND METHODS

Legs, tarsi, and various details were photographed on an FEI Quanta 200 (www.fei.com) scanning electron microscope (SEM). Color photographs were taken under a Leica MZ 12.5 stereomicroscope (www.leica-microsystems.com) with a mounted JVC KY-F70B digital camera (www.pro.jvc.com), where images were captured at different focal planes and then assembled using the application Auto-Montage Pro Version 5.00.0271 by Syncroscopy (www.syncroscopy.com).

We identify specimens using several code numbers, as they have been entered into different databases since their collection. The Natural History Museum of Geneva (MHNG) gave the first code (a sample code), which consists of an area and year abbreviation. The Museum of Comparative Zoology (MCZ) DNA database logs whole collections with identification codes that consist of the prefix "MCZ DNA" and a six-digit number. A Biota database (Colwell, 2004) for Cyphophthalmi in the Giribet Laboratory at the MCZ gives each specimen a different six-digit ID number, with the prefix "SPM." Moreover, this species described here was also used earlier in phylogenetic analysis under the moniker "Peninsula sp. 18" (Clouse *et al.*, 2009; Clouse & Giribet, 2010).

Appendage measurements were not always possible for certain specimens: the first (proximal) cheliceral article must be removed to measure its full length, trochanters can be broken when legs are removed, some individuals have injured or deformed appendages, and in this species in particular, the chelicerae are usually pulled tightly under the overhanging anterior edge of the dorsal scutum, obscuring the dorsal crest. Chelicera depth was measured just proximal to the dorsal crest to a point between the first and second ventral process. The depth of the fourth tarsus was measured on the proximal side of the adenostyle base.

TAXONOMY

FAMILY STYLOCELLIDAE

Leptopsalis foveolata sp. n.

Figs 1-34

HOLOTYPE: MHNG sample TH-99/4, MCZ DNA101093, MCZ Cyphophthalmi database SPM003920; Sai Khao Waterfall, Mt Sankalakheeree, Namtok Sai Khao National Park, ca 20 km NW of Yala city, Pattani Province, Thailand, 6°39'18.5"N, 101°5'50.5"E, 260 m; male; 22-X-1999, leg. P. Schwendinger.

PARATYPES: MHNG sample TH-99/4, MCZ DNA101093, MCZ Cyphophthalmi database SPM003917-9 (Figs 1-3); 3 males; same data as for holotype. – MHNG sample TH-99/4, MCZ DNA101093, MCZ Cyphophthalmi database SPM003921-4 (Figs 4-6); 4 females; same data as for holotype. – MHNG sample TH-99/5, MCZ DNA101496, MCZ Cyphophthalmi database SPM004415; 1 female; 23-X-1999, 260-350 m, otherwise same data as for holotype.

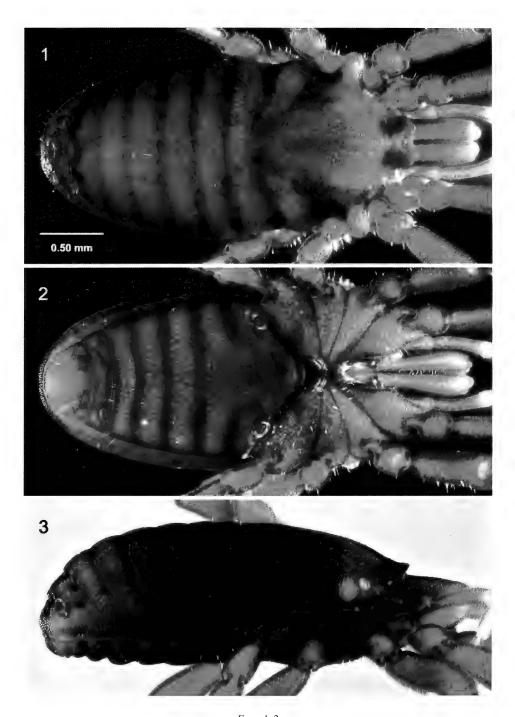
DEPOSITION AND PRESERVATION OF TYPES: All types are deposited in the MHNG except those used for SEM (SPM003918-9), which are deposited in the MCZ Cyphophthalmi SEM collection. Male paratypes SPM003918-9 were mounted for scanning electron microscopy, male paratype SPM003917 and female paratype SPM003922 were dissected to examine genitalia, and female paratypes SPM003921, SPM003922, SPM003924, and SPM004415 had DNA (remaining in MCZ) extracted and sequenced for phylogenetic studies (Clouse *et al.*, 2009; Clouse & Giribet, 2010).

DESCRIPTION: Body length (3.27 mm) of male holotype 2.13 times the maximum width (1.53 mm), equal across the ozophores and the second opisthosomal segment.

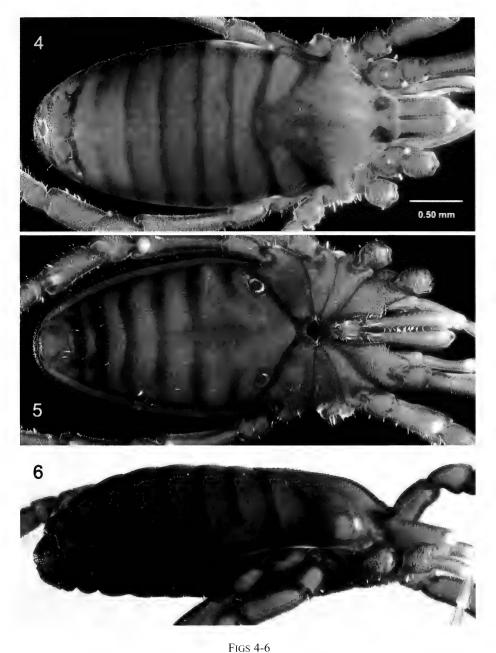
Dorsal scutum (Figs 1, 4, 7): Transverse prosomal-opisthosomal sulcus and opisthosomal sulci distinct; mid-dorsal, longitudinal opisthosomal sulcus absent. Anterior margin of prosoma meeting cheliceral ridge with protruding, weakly bilobed lip, rising gradually; entire scutum weakly arched.

Ventral opisthosoma (Figs 2, 5, 8): Transverse sulci shallow and granular, complete after sternite 3, especially shallow between sternites 3 and 4; first three sulci after tergite 3 weakly sinoidal, medial region bending forward about as far as lateral ends. Sutures between tergites 6 and 7, and 7 and 8 gently curved back laterally.

Pits: Posterior opisthosomal sulci of males and females with deep, granular pits (Figs 7-12), these not corresponding to either tuberculate or microgranular integument ornamentation described by Murphree (1988). Dorsal pits mostly along sulci between tergites VI and VII and between tergites VII and VIII, numbering five in each row (Figs 7, 12). Sulcus between tergites V and VI granular, with small depressions. Ventral pits more irregular, along antertior edges of sternites 7 and 8, resembling deep, uneven folds along the sutures, forming two rows of five and six pits, respectively (Figs 8, 11).

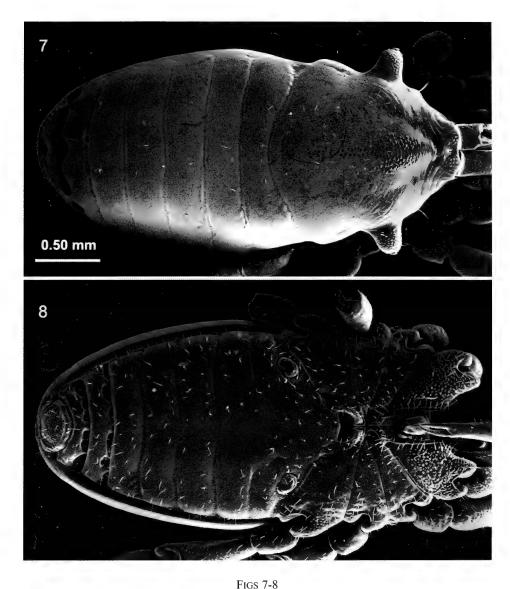


FIGS 1-3
Leptopsalis foveolata sp. n., male paratype SPM003917. (1) Dorsal view. (2) Ventral view. (3) Lateral view.



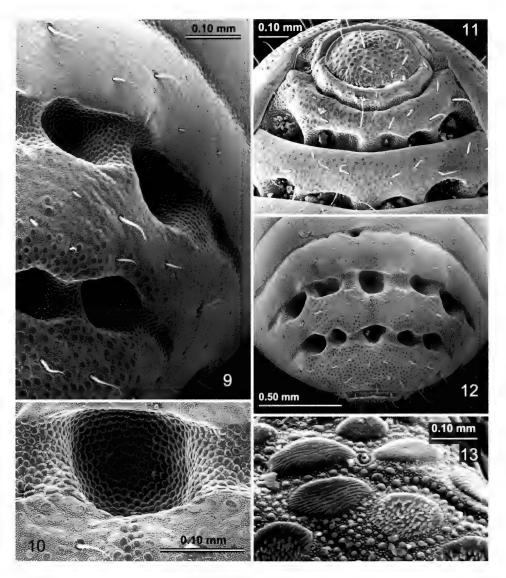
Leptopsalis foveolata sp. n., female paratype SPM003922. (4) Dorsal view. (5) Ventral view. (6) Lateral view.

Tergite IX and sternite 9 with wrinkled, granular edges opposite anal plate (Figs 8, 19). Pits densely covered with large granules, lacking large pores or other structures (Fig. 10).



Leptopsalis foveolata sp. n., scanning electron micrographs of male paratypes SPM003919 and SPM003918, respectively. (7) Dorsal view. (8) Ventral view.

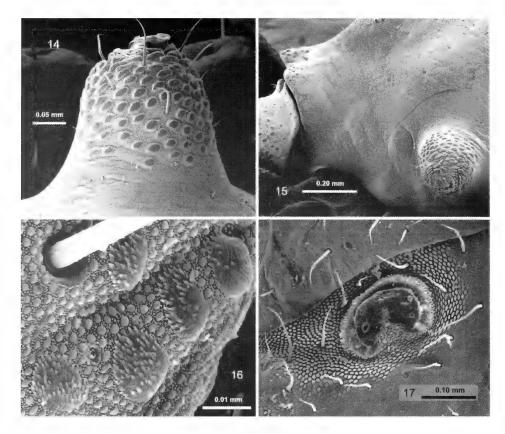
Ozophores, eyes, and sculpturing: Ozophores lateral, raised above carapace edge ("type 2" of Juberthie, 1970), large, tapered, pointing anteriad (Fig. 14). Eyes distinct, large, with cornea, positioned anterior to ozophores (Fig. 15). Integument uniformly microgranular but lacking larger tubercules except in particular locations. Large tubercules of two types: raised, smooth and flattened; and rough, digitate. Transitional tubercles also present around pits (Figs 13, 16). Raised tubercules on dorsal, anterior



Figs 9-13

Leptopsalis foveolata sp. n., magnified views of pits of male paratypes SPM003919 (9-10, 12-13) and SPM003918 (11). (9) Dorsal pits dorsolaterally on right side. (10) Central pit between tergites VI and VII. (11) Ventral pits and anal region. (12) All dorsal pits. (13) Transition of granule morphology along lower left lip of central pit seen in Fig. 10.

edge of carapace; on distal ¾ of ozophores; on central anterior, dorsal prosoma; starting in posterior half and center of tergite VII through tergites VIII and IX; sparsely distributed in center of tergite VI; inside sulcus between tergites V and VI; on anal plate; sparsely distributed on sternite IX; inside, between and lateral to dorsal and ventral pits; inside ventral opisthosomal sulci; on coxae I and extreme distal anterior



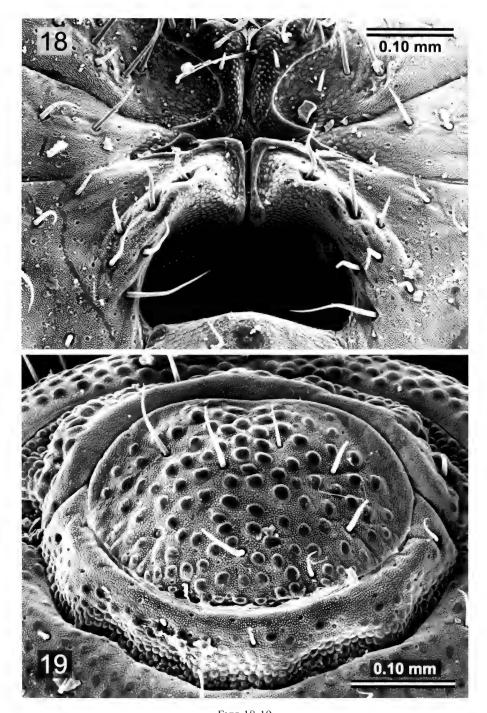
Figs 14-17

Leptopsalis foveolata sp. n., male paratype SPM003919 (14-15) and male paratype SPM003918 (16-17). (14) Ozophore, dorsal view. (15) Base of chelicera, anterior margin of dorsal scutum, eye and ozophore, lateral view. (16) Transition of granule morphology along edge of ventral pit. (17) Spiracle.

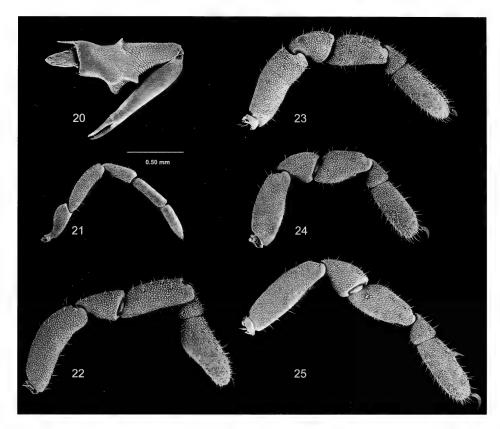
of coxae IV; and on all articles of all appendages except third article of chelicerae. Large flattened, digitate granules found in three longitudinal rows on dorsal side of prosoma; anterior to prosomal-opisthosomal sulcus; starting on tergite VI to anterior of tergite VII; and starting laterally on sternite 3, increasing through sternite 9.

Ventral prosomal complex (Fig. 18): Coxae IV meeting along midline for distance equal to length of gonostome; coxae III not meeting, with weak sternum between proximal ends; contact zone between coxae II longer than that between coxae IV, with endites more than twice as large as those on coxae IV. Gonostome wider than long, evenly arched to rectangular anteriorly; first opisthosomal sternite slightly rounded anteriorly, forming weakly concave posterior edge of gonostome; lateral walls formed by distinct, elevated posteroproximal processes of fourth coxae, these most elevated on anterior edge.

Anal region (Figs 11, 19): Sternites 7, 8 and 9 and tergite IX free; tergite IX wider than sternite 9, both with densely and coarsely granular, uneven surface opposite



Figs 18-19 *Leptopsalis foveolata* sp. n., male paratype SPM003918, details of ventral side. (18) Gonostome and ventral prosomal complex. (19) Anal region.



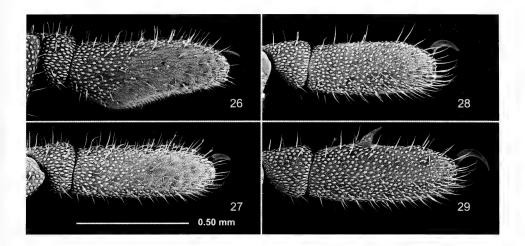
FIGS 20-25

Leptopsalis foveolata sp. n., appendages of male paratype SPM003918, lateral views. (20)
Chelicera. (21) Palp. (22) Leg I. (23) Leg II. (24) Leg III. (25) Leg IV.

anal plate; microgranular, even surface flush along edge of anal plate. Tergite VIII lacking gland pore; anal plate with large, raised granules and irregularly convex surface.

Chelicera (Fig. 20): Third article (movable finger) about one-fourth length of second article, second article gradually narrowing for distal two-thirds of length. First article with distinct dorsal crest, ridge flattening laterally and visible only as smooth area leading to distinct, moderately-sized second ventral process. Dorsal crest often not visible in specimens, usually pulled under anterior edge of dorsal scutum. First (proximal) ventral cheliceral process distinct, slightly larger than second (distal) ventral process. First article with large, evenly spaced granules laterally and dorsally after dorsal crest. Second article with some distinct granules at curve to proximal joint; irregular, flattened granules laterally in proximal half; remainder of second article and third article smooth.

Palp and legs: Palp granular from trochanter to proximal fourth of article IV, without process on trochanter (Fig. 21). Leg I granular to proximal third and dorsal surface of tarsus (Fig. 22); leg II granular to proximal half, dorsal and ventral surfaces of



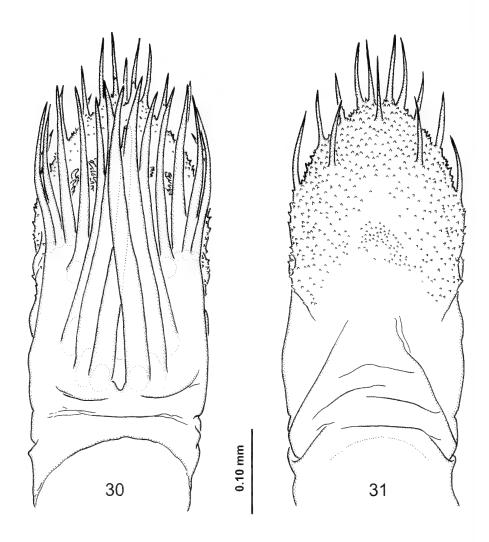
FIGS 26-29

Leptopsalis foveolata sp. n., leg tarsi of male paratype SPM003918, lateral views. (26) I. (27) II. (28) III. (29) IV.

tarsus (Fig. 23); legs III and IV completely granular (Figs 24-25). Tarsus of leg I with distinct solea extending two-thirds length of tarsus (Fig. 26). Medial dorsal surface of tarsi of legs I and II with solenidia (a row of evenly spaced, curved, blunt-tipped sensory hairs; see Willemart & Giribet, 2010), these situated more distally on tarsus I; areas around solenidia generally without granules (Figs 26-27). Tarsus of leg IV evenly granular; depth even for most of its length; adenostyle located at 30% of tarsus length from the proximal end, its tip pointing distally (Fig. 29).

Spermatopositor: Microtrichia formula: 3, 10, 7+7; dorsal microtrichia on two or three different levels, medial three on each side attached distinctly proximally to the lateral four, these about half the length of the former; ventral microtrichia on two levels, medial one near apex of spermatopositor, lateral two more than halfway down to level of most lateral apical microtrichia; four apical microtrichia arranged in two pairs on either side of shallow, apical, medial invagination; remaining six apical microtrichia evenly spaced along sides to just distal of widest point; microtrichia with few denticles proximal on their shafts. Ventral surface of spermatopositor with numerous denticles (Figs 30-31). Gonopore complex with broad lobus medialis lacking lateral processes; short lobuli laterales present, distinctly proximal, not reaching base of lacinia dorsalis, the latter extending distally to just beyond distal edge of lobus medialis, flanked by curved digiti extending the same length as lacinia dorsalis (Fig. 32).

Ovipositor (Figs 33-34): Two apical lobes, each with several setae over whole surface, ending in apical seta; a pair of setae lightly shorter than the apical ones just subapical on each lobe; more subapically a sensitive process containing a dense set of slightly curved, shorter and furcate setae. Distinct pigmented bodies in distal half on prolateral side of each apical lobe. (These pigmented bodies have meanwhile also been found in another *Leptopsalis* sp. and in *Stylocellus globosus* Schwendinger & Giribet in Schwendinger *et al.*, 2004, and are thus not apomorphic for *Fangensis* as postulated



FIGS 30-31 *Leptopsalis foveolata* sp. n., spermatopositor of male paratype SPM003917. (30) Dorsal view. (31) Ventral view.

by Schwendinger & Giribet, 2005). Ventroproximal plates narrow, somewhat triangular, less wide than apical lobes and half their length, carrying three setae each. A pair of sac-like receptacles near base of each apical lobe.

Variation: Females are about 9% longer and wider than males, but have the same body proportions. Among males, body size varies by almost 20%, and among females by around 13%. The longest specimen is female paratype SPM004415 (3.68 mm), which is 25% longer than the smallest male and relatively narrower than other specimens (length 2.3 times the width across the ozophores versus average of 2.1

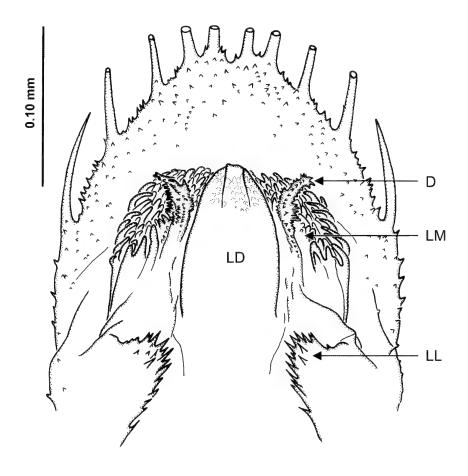
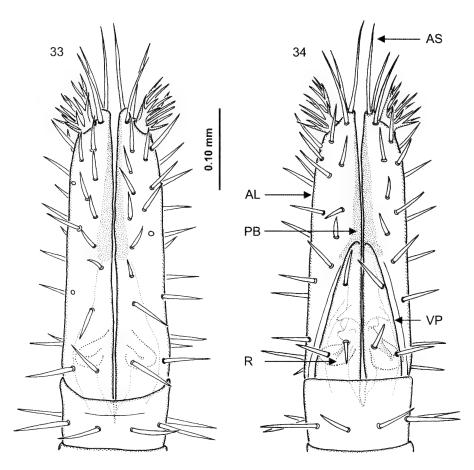


FIG. 32

Leptopsalis foveolata sp. n., gonopore complex of male paratype SPM003917, dorsal view. D = digitus, LM = lobus medialis, LL = lobulus lateralis, LD = lacinia dorsalis.

for males and 2.2 for other females). The number of opisthosomal pits varies as follows: Two male and two female paratypes have 1-2 small but deep pits in the sulcus between tergites V and VI (Fig. 12), others have none. Males (n=4) have five large pits in the sulcus between tergites VI and VII, and between tergites VII and VIII, females (n=5) have 5-6 large pits in each of these sulci. Males have six pits between sternites 6 and 7 and 4-6 pits between sternites 7 and 8, females have 3-6 pits in each of these sulci.

DISTRIBUTION AND HABITAT: The new species is known only from the type locality. The types were collected by sifting and extracting (in Winkler/Moczarski soil extractors) leaf litter and humus from close to the Sai Khao waterfall, in primary lowland rain forest. Soil extractions (by the same method) below the waterfall, along a small side-branch of the stream, in July 2011 yielded no additional specimens.



Figs 33-34

Leptopsalis foveolata sp. n., ovipositor of female paratype SPM003922. (33) Dorsal view. (34) Ventral view. $AL = apical\ lobe, AS = apical\ seta, PB = pigmented\ body, R = receptacle, VP = ventroproximal\ plate.$

DISCUSSION

The literature on Cyphophthalmi systematics has included a rich discussion of their morphological features, and several taxonomic groups have remarkably clear morphological synapomorphies (de Bivort & Giribet, 2004; Giribet & Boyer, 2002; Willemart & Giribet, 2010). Many of these are sexually dimorphic, and of these, most consist of male opisthosomal gland pores and associated modifications such as depressions, apophyses, or "hairy" structures called scopulae. In Stylocellidae, opisthosomal gland pores occur in some species as a single opening on tergite VIII, which is nearly always associated with a longitudinal strip of modified sculpturing on the anal plate. Also, exclusive to Stylocellidae is another sexually dimorphic gland opening, this one on the ventral surface of the male first tarsus in *Fangesis cavernarum* Schwendinger & Giribet, 2005 (see Willemart & Giribet, 2010).

TABLE 1. Lengths, widths (only when specified) and proportions (in brackets) of bodies (= dorsal scuta) and appendage articles of the male holotype and male and female paratype averages. Body proportions are of the dorsal scutum length divided by the corresponding width measurements [across widest part of the body (not counting the ozophores), and across the ozophores], and appendage proportions are the lengths divided by the depths.

A - male l	holotype [ratio]				
Body	Length 3.27	Width (body) 1.53 [2.14]	Width (across ozophores) 1.53 [2.14]	S		
Leg I Leg II Leg III Leg IV	Trochanter 0.31 [1.10] 0.26 [1.06] 0.23 [0.89] 0.33 [1.15]	Femur 0.89 [2.82] 0.76 [2.41] 0.76 [2.52] 0.89 [2.82]	Patella 0.51 [1.71] 0.47 [1.43] 0.37 [1.13] 0.50 [1.59]	Tibia 0.69 [2.40] 0.60 [1.91] 0.51 [1.80] 0.65 [1.99]	Metatarsus 0.27 [1.05] 0.27 [1.12] 0.23 [1.07] 0.26 [1.00]	Tarsus 0.76 [2.31] 0.66 [2.70] 0.66 [3.29] 0.73 [2.43]
Chelicera	I (crest) 0.60 [1.68]	I (whole)	II 1.17 [7.46]	III 0.30 [7.50]		
Palp	Trochanter 0.33 [2.30]	Femur 0.56 [3.55]	Patella 0.36 [2.7]	Tibia 0.41 [4.14]	Tarsus 0.34 [3.43]	
B - male a	average [ratio]	(n = 4)				
Body	Length	Width (body) 1.51 [2.11]	Width (across ozophores) 1.52 [2.10]	3		
Leg I Leg II Leg III Leg IV	Trochanter 0.32 [1.02] 0.25 [0.97] 0.23 [1.06] 0.32 [1.27]	Femur 0.83 [2.96] 0.72 [2.58] 0.70 [2.71] 0.86 [2.90]	Patella 0.47 [1.50] 0.42 [1.31] 0.36 [1.23] 0.45 [1.37]	Tibia 0.66 [2.12] 0.54 [1.69] 0.51 [1.55] 0.59 [1.71]	Metatarsus 0.25 [1.09] 0.25 [0.99] 0.23 [1.30] 0.25 [0.98]	Tarsus 0.71 [2.39] 0.64 [2.84] 0.60 [2.76] 0.70 [2.52]
Chelicera	I (crest) 0.56 [1.60]	I (whole) 0.94 [2.49]	II 1.11 [6.45]	III 0.27 [6.28]		
Palp	Trochanter 0.32 [2.30]	Femur 0.54 [3.77]	Patella 0.32 [2.43]	Tibia 0.38 [3.78]	Tarsus 0.31 [3.02]	
C - female	e average [ration	o] $(n = 5)$				
Body	Length 3.46	Width (body) 1.64 [2.11]	Width (across ozophores) 1.57 [2.21]	S		
Leg I Leg II Leg III Leg IV	Trochanter 0.29 [1.02] 0.26 [0.97] 0.28 [1.06] 0.33 [1.27]	Femur 0.87 [2.96] 0.73 [2.58] 0.74 [2.71] 0.84 [2.90]	Patella 0.45 [1.50] 0.40 [1.31] 0.37 [1.23] 0.44 [1.37]	Tibia 0.59 [2.12] 0.49 [1.69] 0.47 [1.55] 0.53 [1.71]	Metatarsus 0.26 [1.09] 0.23 [0.99] 0.28 [1.30] 0.23 [0.98]	Tarsus 0.74 [2.39] 0.66 [2.84] 0.61 [2.76] 0.71 [2.52]
Chelicera	I (crest) 0.58 [1.89]	I (whole)	II 1.10 [6.51]	III 0.27 [6.37]		
Palp	Trochanter 0.30 [1.98]	Femur 0.51 [3.44]	Patella 0.33 [2.55]	Tibia 0.37 [4.14]	Tarsus 0.34 [3.62]	

Stylocellidae has two other exclusive features that are sexually dimorphic but not readily associated with glandular secretions: Rambla's organ, which is a modified patch of cuticle on the retrolateral side of the fourth tarsus of males in several species (see Rambla, 1994; Schwendinger & Giribet, 2005), and a row of spines on the ventral surface of the first tarsus of *Stylocellus globusus*, which is denser in males than females (Willemart & Giribet, 2010). The feature we describe here, the deep pits near the posterior end of males and females of *L. foveolata* sp. n., is also not apparently glandular in function but is additionally not sexually dimorphic. The only indication that these pits are associated with a liquid is the modification of granules along the posterior edge of each pit row, the grooves and digitate surfaces perhaps used to channel and disperse some compound. The one special feature in Cyphophthalmi this most resembles is Hansen's organ, which is an irregularly grooved raised area of cuticle found on the coxae and more distal leg articles of both males and females in the African genus *Ogovea*. Like Rambla's organ, Hansen's organ has micropores but is not clearly glandular in function (Giribet & Prieto, 2003; Willemart & Giribet, 2010).

Sexually dimorphic features are rare in *Leptopsalis*, the only occurrence being the anal gland pore in a few of the early lineages of the family (Clouse, in press; Clouse *et al.*, 2009). This suggests that there has been a profound behavioral shift in the genus whereby such features are not needed, despite living in a wide variety of habitats and radiating into the largest clade in the family. The pits described here in *L. foveolata* sp. n. show no difference between males and females, and may indicate an adaptation to some novel selection pressure at the type locality. Living near a waterfall, do these animals experience flooding and need these pits to channel water or trap air bubbles? But why then only at their posterior end? If anything, this novel structure highlights how much more there still is to discover about Cyphophthalmi behavior and ecology.

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Ophiotaenia lapata sp. n. (Eucestoda: Proteocephalidea) from Madagascar: a parasite of the endemic snake Madagascarophis colubrinus (Colubridae)

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Abstract: Ophiotaenia lapata sp. n. (Cestoda: Proteocephalidea) from Madagascar: a parasite of the endemic snake Madagascarophis colubrinus (Colubridae). - A new proteocephalidean cestode, Ophiotaenia lapata sp. n., is described from the gut of the endemic colubrid snake Madagascarophis colubrinus (Schlegel, 1837) (Colubridae) from Madagascar. The new species differs from all but one *Ophiotaenia* species parasitic in African snakes by the presence of an apical organ. *Ophiotaenia* lapata differs from O. adiposa Rudin, 1917, which also possesses an apical organ, by the number of testes (89-170 in the new species versus 170-220 in O. adiposa), by the position of the genital pore in relation to the anterior margin (43-53% of proglottis length in O. lapata versus 20-25%) and the scolex width (240-280 µm in the former species versus 500-600 µm in the latter). The new species possesses, unlike all but one *Ophiotaenia* species parasitic in African snakes, a three-layered embryophore. The other African species have two-layered embryophore except for Ophiotaenia georgievi de Chambrier, Ammann & Scholz, 2010, which can be distinguished by the absence of an apical organ, by the number of uterine branches on each side (23-28 in O. georgievi versus 41-68 in O. lapata) and by the total length of the strobila (50 mm in O. georgievi and 295 mm in O. lapata). Ophiotaenia lapata is the third proteocephalidean cestode reported from Madagascar.

Keywords: Eucestoda - taxonomy - morphology - Serpentes - helminths - Africa.

INTRODUCTION

Tapeworms of the order Proteocephalidea Mola, 1928 are frequent and cosmopolitan parasites of freshwater fishes, reptiles and amphibians (Rego, 1994). The genus *Ophiotaenia* La Rue, 1911 comprises ninety-six species parasitic in reptiles and amphibians (for a list of species see Schmidt, 1986; de Chambrier *et al.*, 2010, 2012). Two specimens of the colubrid snake *Madagascarophis colubrinus* (Schlegel, 1837)

endemic to Madagascar were examined in 2011 by the present authors. They harboured proteocephalidean cestodes belonging to *Ophiotaenia*, which are described herein as a new species.

MATERIALS AND METHODS

Snakes examined were killed by injection of Nembutal (sodium pentobarbitone) and immediately dissected. Freshly collected tapeworms were rinsed in a saline solution (0.9% in water), placed in a Petri dish with a small quantity of saline and fixed with hot, almost boiling 4% neutral formalin. After 1-3 weeks, the worms were transferred and stored in 75% ethanol solution. The worms used for morphological study were stained with Mayer's hydrochloric carmine, destained in 75% acidic ethanol (i.e. 75% ethanol with about 2 ml HCl/100 ml), dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted as permanent preparations in Canada balsam. For histology, pieces of the strobila were embedded in paraffin wax, sectioned transversely at 15 µm intervals, stained with Weigert's haematoxylin and counterstained with 1% eosin B acidic solution (see Scholz & Hanzelova, 1998; de Chambrier, 2001; Oros et al., 2010). Eggs were studied in distilled water. Scolex for scanning electron microscopical (SEM) observation was dehydrated in a graded ethanol series (80%, 96%, twice 100%), then transferred to a graded amyl/acetate series, critical point-dried in CO₂, sputter coated with gold and examined with a Zeiss 940A electron microscope at the Natural History Museum, Geneva. Microthrix terminology follows Chervy (2009).

All measurements are given in micrometres unless otherwise indicated. Abbreviations used in the description are as follows: x = mean; n = number of measurements; CV = coefficient of variability (expressed in %); RSO = ratio of the width of the ovary to the width of the proglottis; PGP = position of genital pore (cirrus pore) expressed as percentage of its position to the proglottis length from the anterior margin; RSCS = relative size of the of cirrus-sac expressed as percentage of its length to the width of the proglottis.

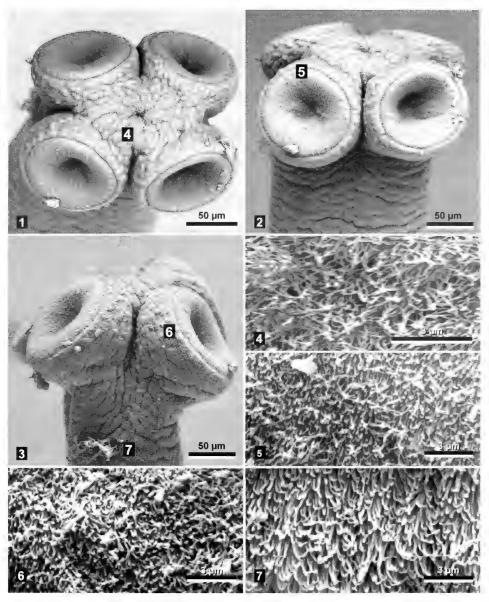
The worms studied were compared with those collected by G. Brygoo, Madagascar Pasteur Institute, between 1960 and 1970. His collection of tapeworms from snakes and amphibians from Madagascar was originally deposited in the Institute of Zoology in Neuchâtel, Switzerland, and then transferred to the Natural History Museum in Geneva. New material studied has been deposited in the helminthological collection of the Natural History Museum, Geneva, Switzerland (acronym MHNG PLAT), in the Department of Animal Biology, Faculty of Sciences, University Antananarivo, department of Animal Biology (acronym UADBA), and in the Institute of Parasitology, České Budějovice, Czech Republic (acronym IPCAS).

RESULTS

Ophiotaenia lapata sp. n.

Figs 1-14

TYPE MATERIAL: Holotype MHNG-PLAT-79567 (field number Mad 007a) (1 slide) and 7 paratypes: MHNG-PLAT-79568 (Mad 007b), 3 whole mounted slides and 18 cross sections; MHNG-PLAT-82165 (Mad 007p), 1 slide; MHNG-PLAT-82166 (Mad 007x), 1 slide, scolex used for SEM; MHNG-PLAT-82167 (Mad 007z), 1 whole mounted slides and 10 transverse sections; MHNG-PLAT-79570 (Mad 008a), 1 whole mounted slide. UADBA No50001 and 50003, (Mad 007), two specimens, 2 slides.



Figs 1-7

Ophiotaenia lapata sp. n. Scanning electron micrographs. Paratype (MHNG-PLAT-82166, field number Mad 007HFx). (1) Scolex, apical view (2) Scolex, dorsoventral view. (3) Scolex, lateral view. (4) Capilliform filitriches at level of the apex of the scolex. (5) Capilliform filitriches and small gladiate spinitriches at marginal surface of sucker. (6) Capilliform filitriches and small gladiate spinitriches at non-adherent surface of sucker (7) Gladiate spinitriches at proliferation zone surface. Scale-bars: $1-3=50~\mu m$; $4-7=3~\mu m$.

OTHER MATERIAL: MHNG-PLAT-82172 (field number Mad 007hf), 2 whole mounted slides, (voucher material used for the study of the eggs). – MHNG-PLAT-82169 (field number Mad 007y), 1 whole mounted slides and 10 transverse sections. – UADBA No50002, 50004

(field number Mad 007), and 50005 (field number Mad 007c), 3 mounted slides. Some pieces of gravid proglottides were placed in alcohol for DNA analyses. – MHNG-PLAT-79569 (Mad 007c); MHNG-PLAT-82175 (Mad 008hf), and IPCAS C-625, 1 whole mounted slide and 4 slides of serial cross sections (from MHNG-PLAT-82175). – MHNG-PLAT-73222, from Brygoo material; Madagascar, Befandriana S., October 1967, 1 whole mounted slide and 13 transverse sections.

TYPE LOCALITY: Ambinda Nord/Beanka (-17.93986°Lat; 44.46822°Long), 18 November 2011. All material listed above is from this locality, except MHNG-PLAT-73222.

DESCRIPTION (based on 8 specimens, 4 complete and 4 incomplete): Proteocephalidae, Proteocephalinae.

Cestodes up to 295 mm long; maximum width 1.2 mm. Strobila acraspedote, anapolytic. All proglottides longer than wide (length: width ratio 1.03-1.52 to 4.80-6.00, from immature to gravid). Scolex 120-150 long and 190-280 (n=3) wide, slightly wider than neck (Figs 1-3, 8). Suckers uniloculate, round, slightly embedded, 85-115 (n=12) in diameter, representing 30-48% of scolex width (Figs 1, 2). Apical organ 40-45 in diameter, i.e. 15-19% of scolex width, surrounded by cells with finely granular cytoplasm (Fig. 8). Proliferation zone 2.5-3.6 mm long and 140-185 wide.

Internal longitudinal musculature weakly developed, anastomosed, formed by numerous tiny muscle fibres (Figs 10, 11). Ventral osmoregulatory canals overlapping testes, reaching laterally vitelline follicles, 5-25 in diameter, with secondary canals directed externally; dorsal canal narrow, thick-walled, 5-10 in diameter (Fig. 13).

Testes medullary, on one layer, in two narrow lateral bands (poral field separated by terminal genitalia to preporal and postporal groups). Testes rarely reach anterior margin of proglottis, but never reach to ovary, occupying 81-88% of total length of proglottis (Figs 10, 13, 14). Testes 89-170 (x = 128, n = 38, CV = 17%) in number, with 47-84 (x = 66) aporal testes, 25-49 (x = 37) preporal testes and 19-38 (x = 29) postporal testes. Testes spherical, 50-65 (x = 55, x = 22) in diameter, degenerated in gravid proglottides (Fig. 14).

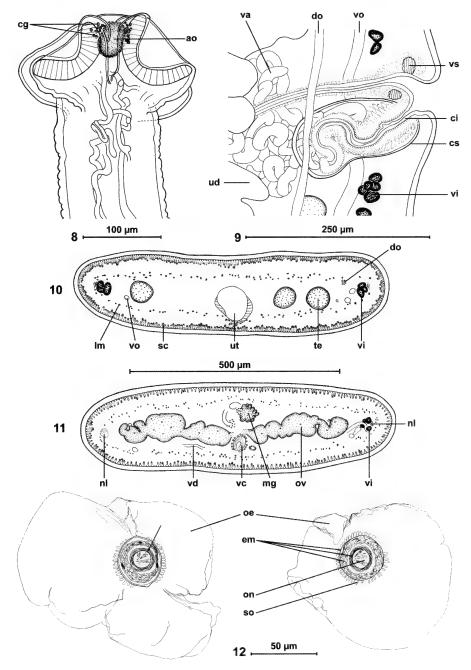
Cirrus-sac elongate, thick-walled, 170-250 (x = 210, n = 53) long and 75-90 (x = 80, x = 10) wide (Fig. 9); RSCS 19-26 % (x = 22%, x = 53, CV = 8 %). Cirrus length represents about 70% of cirrus-sac length. Vas deferens strongly coiled, situated between proximal part of cirrus-sac and midline of proglottides, but never crossing it.

Genital atrium present; genital pores alternating irregularly, more or less equatorial, PGP = 43-53% (x = 49%, n = 12, CV = 6%) (Figs 13, 14). Genital ducts passing between osmoregulatory canals.

Ovary medullary, bilobed (Figs 11, 13, 14), 520-840 wide, RSO = 68-81% (x = 75%; n = 55; CV = 4%). Mehlis' glands 50-80 (x = 60, n = 9) in diameter, representing 9-12% of proglottis width (Figs 11, 13, 14).

Figs 8-12

Ophiotaenia lapata sp. n. (8) Holotype, scolex, dorsoventral view (MHNG-PLAT-79567). (9) Paratype, vagina and cirrus-sac region, dorsal view (MHNG-PLAT-79568). (10-11) Transverse sections of a mature proglottis at level of anterior part and ovary, respectively (MHNG-PLAT-82167). (12) Eggs drawn in distilled water showing the three-layered embryophore (MHNG-PLAT-82172); additional layer marked by an arrow. Abbreviations: ao – apical organ; cg – cells with finely granular cytoplasm; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em



- embryophore; lm - internal longitudinal musculature; mg - Mehlis glands; nl - longitudinal nerve; oe - outer envelope; on - oncospheres; ov - ovary; sc - subtegumental cells; so - small outgrowths; te - testes; ud - uterine diverticles; ut - uterus; va - vas deferens; vc - vaginal canal; vd - vitelloduct; vi - vitelline follicles; vo - ventral osmoregulatory canals; vs - vaginal sphincter. Scale-bars: 8 = 100 μm ; 9 = 250 μm ; 10–11 = 500 μm ; 12 = 50 μm .

Vitelline follicles medullary, arranged in two lateral fields near margins of proglottides, occupying 90-95% of proglottis length, interrupted at level of cirrus-sac (Figs 13, 14).

Vaginal canal forming small seminal receptacle anterodorsal to ovarian isthmus. Terminal part of vaginal canal (pars copulathrix vaginae) surrounded by large vaginal sphincter and chromophilic cells (Fig. 9). Vagina anterior (62%; n = 26) or posterior (38%) to cirrus-sac.

Primordium of uterine stem medullary, present in immature proglottides. Development of uterus of type 1 according to de Chambrier *et al.* (2004): in immature proglottides, uterine stem straight, occupying most length of proglottis but never crossing ovarian isthmus, formed by wide longitudinal band of chromophilic cells situated along midline of proglottides. Lumen of uterus appearing in first mature proglottides (Fig. 13); diverticula (lateral branches) formed before first eggs appear in uterine stem. In pregravid proglottides, uterus occupying up to 33% of proglottis width, with 41-68 thin-walled lateral diverticula on each side. In gravid proglottides, diverticula occupying up to 80% of proglottis width. Uteroduct enters uterus almost at level of ovary isthmus.

Eggs round, with outer envelope 140-165 in diameter (Fig. 12). Embryophore spherical, with thick supplementary spherical layer between outer envelope and oncosphere, thus forming three-layered embryophore: internal layer 18-20 (n=8) in diameter, middle layer 29-33 (n=7) in diameter; external layer 34-39 (n=8) in diameter; External layer of embryophore covered by small outgrowths 2.5-4 long; oncosphere spherical, 14-15 in diameter (n=8), with three pairs of hooks, 8-9 long (Fig. 12). Eggs mature very fast in uterus and ripe eggs (oncospheres with hooklets) are present in the first pregravid proglottides.

TYPE HOST: *Madagascarophis colubrinus* (Schlegel, 1837) (Serpentes, Lamprophiidae).

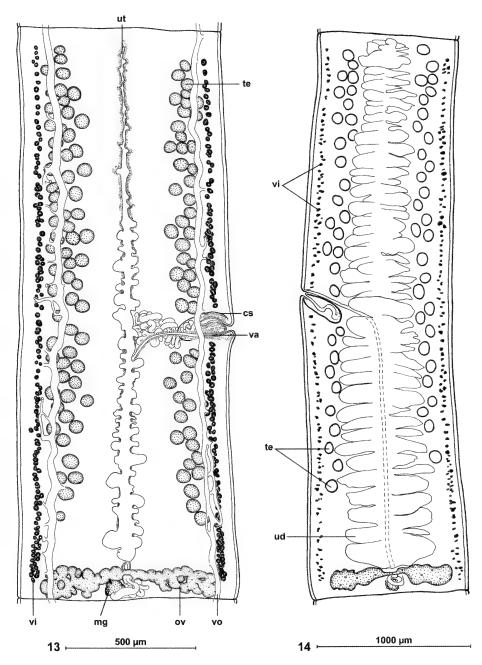
SITE OF INFECTION: Intestine.

PREVALENCE: 2/2 (100%).

ETYMOLOGY: The new species is named after the vernacular local name of the host, i.e. "lapata".

DIFFERENTIAL DIAGNOSIS: The new species is placed in *Ophiotaenia* La Rue, 1911 (Proteocephalinae) because of the medullary position of the vitelline follicles, the unarmed scolex with uniloculate suckers and testes forming two separate fields (Schmidt, 1986). Ninety-six species of *Ophiotaenia* parasitizing reptiles and amphibians are currently recognized as valid (Freze, 1965; Schmidt, 1986; Ammann & de Chambrier, 2008; Marsella & de Chambrier, 2008; Coquille & de Chambrier, 2008; de Chambrier & de Chambrier, 2010; de Chambrier *et al.*, 2010, 2012). Out of these, 64 species are parasites of snakes (Squamata) (see Table 1 in de Chambrier *et al.*, 2010).

According to Freze (1965), the species of *Ophiotaenia* are limited in their distribution to individual continents and/or zoogeographical regions; this assumption has been then supported by other data, like an high degree of isolation determined by the presence of a number of endemic genera such as *Marsypocephalus*, *Sandonella* (both



Figs 13-14

Ophiotaenia lapata sp. n. (13) Paratype, mature proglottis, ventral view (MHNG-PLAT-79568). (14) Paratype, schematic view of a gravid proglottis, ventral view (UADBA No 50001). *Abbreviations*: cs – cirrus-sac; mg – Mehlis glands; ov – ovary; te – testes; ud – uterine diver – ticles; ut – uterus; va – vagina; vi – vitelline follicles; vo – ventral osmoregulatory canals. Scalebars: 13 = 500 μm; 14 = 1000 μm.

Africa), and *Goezeella* (South America) for fish parasites and *Rostellotaenia* (Africa), *Acanthotaenia* (Asia) and *Kapsulotaenia* (Australia, Papua New Guinea) for reptiles parasites (Freze, 1965); furthermore, for species of *Ophiotaenia* from amphibian hosts (de Chambrier *et al.*, 2006) and from reptilian hosts (Ammann & de Chambrier, 2008), a strict specificity (oioxenous sensu Euzet & Combes, 1980) was observed in all species of this genus. For this reason, the new species is separable from 14 *Ophiotaenia* species found in snakes in Africa (for their complete list, see de Chambrier *et al.*, 2010).

Ophiotaenia lapata sp. n. differs from all but one Ophiotaenia species parasitic in African snakes by the presence of an apical organ (Table 1), the only African species possessing an apical organ being O. adiposa Rudin, 1917 described from Bitis arietans from Cameroun. Ophiotaenia lapata differs from O. adiposa by its lower number of testes (89-170 versus 170-220), position of the genital pore (situated at 43-53% of the proglottis length from the anterior margin, i.e. almost equatorial in O. lapata, versus markedly pre-equatorial, i.e. at 20-25% length of the proglottis in O. adiposa) and smaller scolex (width 240-280 μm in the former species versus 500-600 μm in O. adiposa) (Table 1).

Ophiotaenia lapata n. sp. also differs from all but one Ophiotaenia species parasitic in African snakes in the possession of a third layer of the egg embryophore (Fig. 12). This layer is external to the oncosphere, i.e. it forms the internal envelope of the embryophore. The eggs of all African taxa described until now possess only a two-layered embryophore (Beddard, 1913; Rudin, 1917; Fuhrmann, 1924; Sandground, 1928; Hilmy, 1936; Mettrick, 1960, 1963; Southwell & Lake, 1939; Freze, 1965). A similar structure, i.e. an additional layer of the embryophore, was first observed in some other Proteocephalidea tapeworms (see de Chambrier & Vaucher, 1999; de Chambrier, 2006; Coquille & de Chambrier, 2008; Marsella & de Chambrier, 2008; de Chambrier et al., 2010; de Chambrier & de Chambrier, 2010; de Chambrier et al., 2012).

This character is present in a wide range of proteocephalidean genera and geographical areas, such as *Proteocephalus* (*P. hobergi* de Chambrier & Vaucher, 1999) in Paraguay, *Kapsulotaenia* (*K. sandgroundi* Carter, 1943) in Indonesia, *Cairaella* (*C. henrii* Coquille & de Chambrier, 2008) in Ecuador, *Ophiotaenia* (*O. alessandrae* Marsella & de Chambrier, 2008 in Ecuador, *O. gallardi* (Johnston, 1911) in Australia and *O. bungari* de Chambrier, Binh & Scholz, 2012 in Vietnam). This additional layer of the embryophore, even if it seems to be a convergence phenomenon, is considered as a good discriminant character.

The only African species, the embryophore of which is also three-layered as in the eggs of *O. lapata*, is *O. georgievi* de Chambrier, Ammann & Scholz, 2010 described recently from *Leioheterodon geayi* Mocquard. This species differs from *O. lapata*, besides being devoid of an apical organ (see above and Table 1), by the number of uterine branches (23-28 in *O. georgievi* versus 41-68 in *O. lapata*), and by the total length of the strobila (50 mm in *O. georgievi* versus 295 mm in *O. lapata*).

Table 1. Species of Ophiotaenia from reptiles in Africa (modified from de Chambrier et al., 2010)

Species	Number of testes	RSCS	Position of the genital pore	Position of the vagina	Apical organ	Width of scolex	Total body length (mm)	Uterine branches on each side	Diameter of eggs
O. adiposa O. congolensis	170-220 65	26%*	20-25% 44-47%*	ant-post	yes	500-600	300-400 80	40-50	12*
O. crotaphopeltis	94-98	14%*	54%*	i	ou	160-180	not given	15-18	26
O. gabonica	130-123	18-20%	30%: 42%*	post-ant generally post	011	300-600	> 380	48-33 38-46	39
O. georgievi	92-140	19-32%	44-56%	post-ant	no	225-235	50	23-28	31-35
O. meggitti sp. inq.	86-104	33%	*%05	usually ant.	ċ	not given	89 <	35	25
O. monnigi sp. inq.	80	10-11%	51%*	ant	ċ	no scolex	50	50-57	30
O. nigricollis	176-210	20-22%	38%*	ant-post	no	300-310	170	16-20	26-33
O. nybelini	06-29	16-20%	47%*	ant-post	no	105	52	25-40	25
O. ophiodex	110-120	22-25%	>20%	ant-post	no	790-1140	210-270	30-42	27-36
O. southwelli	170-230	46-50%*	\$0-55%*	ant-post	no	1500	06	8 to 12	30
O. theileri	160-310	20-25%	41-50%*	ant-post	no	400	estimated 300	35-40	18**
O. zschokkei	160-200	20-25%	%05	usually ant.	no	400	estimated 550-600		18**
O. lapata sp. n.	89-170	19-25%	43-53%	post-ant	yes	190-280	295	41-68	34-39

Abbreviations: RSCS = relative size of the cirrus-sac expressed as percentage of its length to the width of the proglottis from the anterior margin; * - taken from figures in Freze (1965); ** - diameter of oncosphere.

TABLE 2. Cestodes parasites of reptiles and amphibiens from Madagascar (Coll. Brygoo)

No	Host	Genus	species	locality	Date	Parasites	No MHNG-PLAT-
181/62	R.219 R.632	Chalanodon Ithvevphus	madagascariensis sp.	St Augustin Perinet	7.1962 2.1968	Oochoristica sp. Deblocktaenia sp.	73278 73277
89/20	R.638 R 290	Lioheterodon Lioheterodon	geayi modestus	Antananarivo Tanandava	4.1968	Ophiotaenia georgievi Cestode	65470 - 65477
28/61	R.63	Lioheterodon	. –	Ejeda-Betioky	4.1961	Ophiotaenia sp. 1	62581
69/88	R.667	Lioheterodon	modestus	Befandriana	12.1969	Ophiotaenia sp. 1	73261
19/661	R.171	Liopholidophis	lateralis	Tana	11.1961	Ophiotaenia sp. 2?	
48/64	R.409	Liopholidophis	sexlineatus	Andramasina	2.1964	Ophiotaenia sp. 2	73260
181/67 a	R.628	Madagascariophis	colubrina	Befandriana	10.1967	Ophiotaenia lapata	73222
181/67 b	R.628	Madagascariophis	colubrina	Befandriana	10.1967	Ophiotaenia sp. 3	73225
183/67	R.629	Mimophis	mahafalensis	Plateau Mahafaly	10.1967	Ophiotaenia sp. 4	73276
29/65	R.242	Mimophis	_	Lac Bemanta	10.1962	Ophiotaenia sp. 4	73282
208/63	R.291	Sanzinia	_	Ambavaniasy	4.1963	Ophiotaenia sp. 5	73279
71/70		Anodonthyla	montana	Andringitra	1.1971	Ophiotaenia sp. 6	73267
78-70	R.678	Lioheterodon	geayi	Antananarivo	4.1968	Ophiotaenia georgievi	73212
62//65	R.531	Madagascariophis	colubrina	Befandriana	8.1965	Ophiotaenia sp. 3	73274
By 187		Rana	mascareniensis	Maintirano		Ophiotaenia sp. 7	73273

DISCUSSION

Glaw & Vences (1994) and Vences et al. (2009) listed about 300 species of reptiles in Madagascar, most of them (92%) being endemic. Up to now, only two proteocephalidean cestodes, Deblocktaenia ventosaloculata (Deblock, Rosé & Broussart, 1962), and Ophiotaenia georgievi de Chambrier, Ammann & Scholz, 2010, were described from these reptiles (Freze, 1965; de Chambrier et al., 2010). Ophiotaenia lapata n. sp. is the third species of proteocephalideans and the second member of Ophiotaenia reported from this country. However, it is evident that the richness of cestode fauna of reptiles in Madagascar is poorly known and it is reasonable to expect that it is much higher than indicated by the available data.

Samples of Cestodes from reptiles and amphibians collected by G. Brygoo have been deposited in the Natural History Museum in Geneva. Nine endemic hosts were found to be infected with proteocephalidean cestodes (Table 2). The material collected by G. Brygoo between 1961 and 1970 in Madagascar in reptiles and amphibians is particularly rich. A preliminary evaluation of these specimens has indicated that there are probably as many as seven unnamed species and that each of them occurs in only one host species, thus exhibiting a strict specificity (oioxene type sensu Euzet & Combes, 1981) (see Table 2 and de Chambrier *et al.*, 2010). One host, *Madagas - carophis colubrinus*, probably harbours two different cestode species, i.e. *O. lapata* and another species of *Ophiotaenia* (designated as *Ophiotaenia* sp. 3 in Table 2), which bears a huge apical organ.

The taxonomic evaluation has also shown that only few of these seven potentially new *Ophiotaenia* species can be described because they are not well enough preserved to enable a morphological description. In addition, the specimens were fixed with formalin and thus are unsuitable for phylogenetic studies using molecular data. It is thus obvious that new material should be collected in order to better describe the still hidden diversity of reptilian parasites in Madagascar and to elucidate their phylogenetic relationships.

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Ophiotaenia oumanskyi sp. n. (Eucestoda: Proteocephalidea), a parasite of *Lepidobatrachus laevis* Budgett, 1899 (Anura: Leptodactylidae) from Paraguay

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Ophiotaenia oumanskyi sp. n. (Eucestoda: Proteocephalidea), a parasite of Lepidobatrachus laevis Budgett, 1899 (Anura: Leptodactylidae) from Paraguay. - A new species of Ophiotaenia, O. oumanskyi sp. n., is described from the intestine of the frog, Lepidobatrachus laevis (Anura: Leptodactylidae), from Paraguay. Among the 10 species of Ophiotaenia found in anurans of the Neotropical Region, only O. bonariensis Szidat & Soria, 1954 and O. ecuadoriensis Dyer, 1986 possess an apical organ, whereas it is absent in the 8 other species. O. bonariensis differs from O. oumanskyi by the total length of the strobila (400-500 mm versus 50-96 mm) and by the number of testes (120-140 versus 85-119). O. ecuadoriensis differs of O. oumanskyi by the total length of strobila (29 mm versus 50-96 mm), by the position of the vagina to cirrus-sac (posterior versus anterior and posterior) and by the diameter of the embryophore (23-26 versus 30). *Proteocephalus* bufonis Chandra & Gupta, 2007 becomes Proteocephalus chandrae nom. nov. (to avoid homonymy with Proteocephalus bufonis Vigueras, 1942). Proteocephalus chandrae nom. nov. is transferred to Ophiotaenia and becomes Ophiotaenia chandrae n. comb.

Keywords: New species - Proteocephalidae - *Ophiotaenia chandrae* **nom. nov.**

INTRODUCTION

The cestodes of the order Proteocephalidea Mola, 1928 are parasites of freshwater fishes, amphibians, reptiles and marsupials (Schmidt, 1986; Rego, 1994, Cañeda-Guzmán *et al.*, 2001), with the highest species richness in pimelodid fishes in the Neotropical Region (de Chambrier & Vaucher, 1999; Rego *et al.*, 1999, de Chambrier *et al.*, 2006). In contrast, amphibians are scarcely represented as the definitive hosts of proteocephalidean cestodes (de Chambrier *et al.*, 2006; Marsella & de Chambrier, 2008). During a herpetological survey in Paraguay between 1979 and 2002 conducted by the Geneva Natural History Museum, proteocephalidean tapeworms

belonging to *Ophiotaenia* La Rue, 1911, were found in a leptodactylid frog *Lepidobatrachus laevis*. Since this cestode differs from all 24 species of the genus described from amphibians in the world, it is described as a new taxon herein.

MATERIALS AND METHODS

One specimen of *Lepidobatrachus laevis* Budgett, 1899 examined was killed by immersion in a 1% MS 222 solution (Methanesulfonate salt, Sigma, No A-5040) and immediately dissected. The digestive tract was fixed with hot 4% neutral formalin and subsequently stored in 75% ethanol. Strobila was stained with Mayer's hydrochloric carmine, dehydrated in a graded series of ethanol, cleared in eugenol (clove oil), and mounted as permanent preparations in Canada balsam. For histology, pieces of strobila were embedded in paraffin wax, transversely sectioned at 12-15 µm intervals, stained with Weigert's hematoxylin and counterstained with 1% eosin B (acidified with five drops of pure acetic acid for 100 ml solution) following recently updated protocols (see de Chambrier, 2001; Oros et al., 2010). Eggs were studied in distilled water. The specimens have been deposited in the helminthological collection of the Natural History Museum, Geneva, Switzerland (PLAT). All measurements are given in micrometres unless otherwise indicated. For two-dimensional measurements, length is given before width. Amphibian classification and authorities follow Amphibian Species of the World 5.5 (Frost, 2011). Abbreviations used in descriptions are as follows: x, mean; n, number of measurements; RSO, ratio of the width of the ovary to the width of the proglottis; PGP, position of genital pore expressed as percentage of its position to the proglottis length from the anterior margin; RSCS, relative size of the cirrus-sac expressed as percentage of its length to the width of the proglottis; CV, coefficient of variation. Museum abbreviations used are as follows: MHNG, Geneva Natural History Museum, Invertebrate Collection (PLAT), Geneva, Switzerland.

RESULTS

Ophiotaenia oumanskyi sp. n.

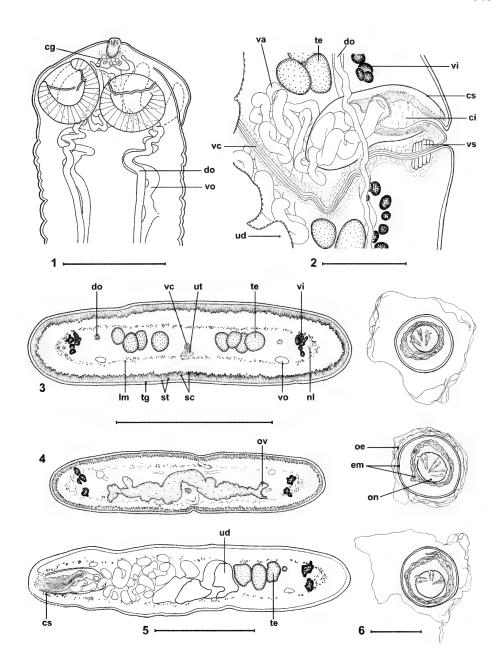
Figs. 1-8

TYPE MATERIAL: Holotype MHNG-PLAT-62560, 1 whole mounted slide. – Paratype 1, MHNG-PLAT-82004, 1 whole mounted slide. – Paratype 2, MHNG-PLAT-82005, 3 whole mounted slides, 10 cross sections. All material is from the type locality and was collected by Carlo Dlouhy 4.02.2002, field number Py 9044.

DESCRIPTION (BASED ON THREE ENTIRE SPECIMENS): Proteocephalidae, Proteocephalinae. Large-sized worms, 50-96 mm long, up to 1.23 mm wide, flattened dorsoventrally, with last proglottides elongated. Strobila acraspedote, anapolytic, with about 150 proglottides; 101-138 (x=125) immature proglottides (up to appearance of spermatozoa in vas deferens), 5-9 (x=7) mature proglottides (up to appearance of eggs in uterus), 2-6 (x=4) pregravid proglottides (up to appearance of hooks in oncospheres);

Figs 1-6

Ophiotaenia oumanskyi sp. n. from Lepidobatrachus laevis. (1) MHNG-PLAT-62560, holotype 1. Scolex, dorsoventral view. (2) MHNG-PLAT-82004, paratype. Cirrus-sac and vagina, dorsal view; note the presence of a vaginal sphincter. (3) MHNG-PLAT-82005, paratype. Mature proglottis, transverse section at posterior part level. (4) MHNG-PLAT-82005, paratype. Mature proglottis, transverse section at ovarian level. (5) Cross-section of gravid proglottis, at level of anterior part (6) MHNG-PLAT-82005, paratype 2. Eggs drawn in distilled water.



Abbreviations: cg = glandular cells, probably of exocrine type, ci = cirrus, cs = cirrus-sac, do = dorsal osmoregulatory canal, em = embryophore, lm = internal longitudinal musculature, ln = longitudinal lateral nerves, oe = outer envelope, on = oncosphere, ov = ovary, sc = subtegumental cells; st = subtegumental muscle fibres, te = testes, tg = tegument, ud = uterine diverticula, ut = uterus, va = vas deferens, vc = vaginal canal, vi = vitelline follicles, vo = ventral osmoregulatory canal, vs = vaginal sphincter. Scale-bars: 1, 5 = 250 μ m; 2 = 100 μ m, 3-4 = 500 μ m, 6 = 20 μ m.

10-17 (x = 13) gravid proglottides. Proliferation zone, 1000-1400 long. Immature proglottides wider than long; and mature, pregravid, gravid proglottides longer than wide. Last gravid proglottides elongated (length: wide ratio 2.3-5.7).

Scolex spherical, 350-410 wide, contains numerous cells with granular inclusions in the apical region. Apical organ present, 38-56 (x = 43) × 50-65 (x = 54, n = 3), ratio of the width of the apical organ to the width of the scolex 14-17%. Four small uniloculate suckers, 150-170 in diameter (Fig. 1).

Internal longitudinal musculature developed (Figs 3-5), forming small anastomosed bundles of muscular fibres. Osmoregulatory canals usually situated between vitellaria and testes. Ventral canal rarely overlapping vitellaria. Ventral canals 25-50 in diameter, with secondary canals ending beneath the tegument; dorsal canals 10-15 in diameter (Figs 1, 3-5).

Testes medullary, oval, 60-75 (x = 70) × 35-45 (x = 40, n = 21) in diameter, numbering 85-119 (x = 103, n = 21, CV = 8%), in one or two layers, in two lateral fields between anterior margin and preovarian space, reaching to ovary (Figs 4, 7), degenerated in last gravid proglottides. Occasionally, some testes overlap uterine stem. Vas deferens coiled, thin-walled, reaching to midline of proglottis (Figs 5, 7). Cirrussac elongate to pyriform, thick-walled, 180-260 long, representing 20-27% (x = 23%, n = 25, CV = 8%) of proglottis width. Cirrus occupying up to 70% of cirrus-sac length (Fig. 2).

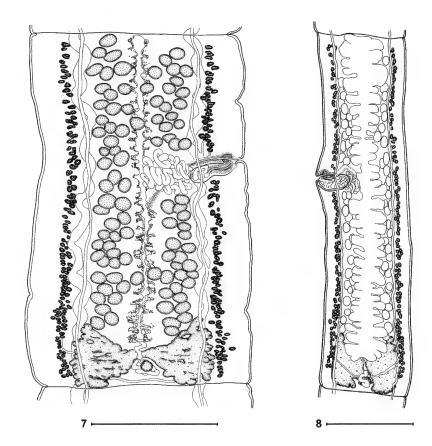
Genital ducts passing between osmoregulatory canals. Genital atrium present. Genital pores irregularly alternating, situated at 35-61% (x = 41%, n = 21, CV = 14%) of proglottis length.

Vagina posterior (in 52% of the proglottides) or anterior (in 48% of the proglottides, n=46) to cirrus-sac, in proximal part lined with intensely staining cells. Muscular terminal sphincter present, 35-40 in diameter (Figs 2, 7, 8). Mehlis' glands 70-105 in diameter, 9-13% of proglottis width.

Ovary medullary, bilobed, small, with follicles on ventral side 445-620 wide, occupying 61-70% (x = 66%, n = 29, CV = 4%) of proglottis width (Figs 4, 7, 8). Ovary occupying 6.7% of proglottis surface in mature proglottis and 8.3% of proglottis surface in gravid proglottis (see Ammann & de Chambrier, 2008 and de Chambrier *et al.*, 2012 for methodology of measuring the ovarian surface).

Vitelline follicles medullary, oval to elongate, in two lateral fields, interrupted porally by vagina and cirrus-sac, reaching almost anterior and posterior margins of proglottides, occupying porally 91-97% and aporally 91-96 % of proglottis length, respectively (Figs 3-5, 7, 8).

Anlage of uterus medullary, already present in immature proglottides. Uterus with 18-25 (n = 13) dorsolateral diverticula on each side in gravid proglottides (Figs 5, 6). Formation of uterus of type 1 according to de Chambrier *et al.* (2004): uterine stem with tubular concentration of numerous intensely stained cells and with lumen in last immature and first mature proglottides (Fig. 7). In mature proglottides, thin-walled lateral diverticula appear, with distal part lined with some intensely staining cells. At this stage, uterus occupying up to 22% of proglottis width. In pregravid proglottides, eggs completely filling uterine stem and diverticula that occupy up to 34% of proglottis width. In gravid proglottides, thin-walled digitate diverticula growing laterally,



Figs 7, 8

Ophiotaenia oumanskyi sp. n. from *Lepidobatrachus laevis*. (7) MHNG-PLAT-62560, holotype, mature proglottis, dorsal view. (8) MHNG-PLAT-82004, paratype. Gravid proglottis, ventral view. Scale-bars: 7, $8 = 500 \mu m$.

occupying up to 72% of proglottis width, opening ventrally by several longitudinal apertures.

Eggs spherical, with thin, hyaline outer envelope, up to 55 in diameter; inner envelope consisting in two-layered embryophore, with external thick layer, 23-26 in diameter and nucleate irregular envelope, 18-21 in diameter; oncospheres 11-13 in diameter, with 3 pairs of embryonic hooks, 6-8 long (Fig. 6).

TYPE LOCALITY: Loma Plata, Filadelfia, Alto Paraguay Province, Paraguay (22°18'S, 68°18'W).

TYPE-HOST: Lepidobatrachus laevis Budgett, 1899 (Leptodactylidae).

SITE OF INFECTION: Intestine.

PREVALENCE: 1/1.

INTENSITY: 3 specimens.

ETYMOLOGY: The new species is named in honour of Igor Oumansky, Geneva, who facilitated our field work in South America.

DIFFERENTIAL DIAGNOSIS: The new species belongs to the genus *Ophiotaenia* because of the medullary position of gonads, the presence of four simple unilocular suckers and two lateral field testes (Freze, 1965; Schmidt, 1986; Rego, 1994).

Off the approximately 96 currently recognized species of *Ophiotaenia* parasitizing reptiles and amphibians (Schmidt, 1986; de Chambrier *et al.*, 2006; Marsella & de Chambrier, 2008; de Chambrier *et al.*, 2010, 2012), 25 species of *Ophiotaenia* parasitize amphibians and 10 of them occur in anurans in the Neotropical Region (Caribbean, southeastern Mexico, Central America and South America; Table 1) (Parodi & Widakowich, 1916; Vigueras, 1942; Wolffhügel, 1948; Szidat & Soria, 1954; Flores-Barroeta, 1955; Dyer & Altig, 1977; Dyer, 1986; Puga & Formas, 2005; de Chambrier *et al.*, 2006; Marsella & de Chambrier, 2008).

Among the 10 species of *Ophiotaenia* found in anurans of the Neotropical Region, only *O. bonariensis* Szidat & Soria, 1954 and *O. ecuadoriensis* Dyer, 1986 possess an apical organ, whereas it is absent in *O. alessandrae* Marsella & de Chambrier, 2008; *O. bonneti* de Chambrier, Coquille & Brooks, 2006; *O. bufonis* (Vigueras, 1942); *O. calamensis* Puga & Formas, 2005; *O. ceratophryos* (Parodi & Widakowich, 1916); *O. hernandezi* (Flores-Barroeta, 1955); *O. noei* Wolffhügel, 1948; and *O. olseni* Dyer & Altig, 1977. The new species resembles *O. ecuadorensis* in the size of the scolex (350-410 μm and 370-450 μm, respectively), but differs in the total length (50-96 mm vs. 29 mm), the position of the vagina to the cirrus-sac (anterior and posterior vs. only posterior) and the diameter of oncospheres (23-26 μm vs. 30 μm). *Ophiotaenia oumanskyi* is easily differentiated from *O. bonariensis* because the latter is very large (400-500 mm versus 50-96 mm), has a higher number of testes (120-140 versus 85-119) and the vagina is always anterior to the cirrus-sac versus anterior and posterior (see Table 1).

On the basis of the above differences, specimens found in *Lepidobatrachus laevis* are considered to represent a new species and the name *Ophiotaenia oumanskyi* sp. n. is proposed to accommodate it.

DISCUSSION

Ammann & de Chambrier (2008) used for the first time the relative ovarian size (the ratio of the ovarian size in relation to that of the entire proglottis) as a useful character that discriminates all known species of *Ophiotaenia* parasitizing reptilian hosts in the New World from species of Palaearctic *Proteocephalus* parasitizing freshwater fishes. They found that all species of *Ophiotaenia* possess a very small ovary, with the relative size of the ovary varying between 1.9 and 5.5%, whereas that of *Proteocephalus* species is much larger (relative size 13.0-19.7%) (see Table 2 in Ammann & de Chambrier, 2008). Later, de Chambrier *et al.* (2012) calculated this character for all *Ophiotaenia* spp. from reptilian hosts (66 species) and for all remaining *Proteocephalus* spp. from freshwater fish hosts (69 species).

The relative ovarian size was newly calculated for 25 species of *Ophiotaenia* from amphibians hosts (Table 2) and was found to vary between 4.5% and 10.8% (x =

TABLE 1. List of species of Ophiotaenia from Neotropical amphibians

Parasite species	Host	Land	Number of testes	RSCS	PGP	Vagina	Apical organ	Apical Scolex organ width	Total length (mm)	Uterine	Eggs dimen- sions	Testi- cular field
Ophiotaenia alessandrae Marsella & de Chambrier, 2008	Hypsiboas boans (Hylidae)	Ecuador	86-128	11-17%	35- 53%	posterior- anterior	ou	475	138	18-25 on each side	22-24	2
O. bonariensis Szidat & Soria, 1954	Leptodactylus latrans (Leptodactylidae)	Argentina	120-140		30%	anterior	yes	800	400-500	23-27 on each side	20-27	2
O. bonneti de Chambrier, Coquille & Brooks, 2006	Lithobates vaillanti (Ranidae)	Costa Rica 100-177	100-177	15-24%	15- 29%	anterior	no	280- 385	380	18-32 on each side	25-30	2
O. bufonis (Vigueras, 1942)	Peltophryne peltacephalus (Bufonidae)	Cuba	141-191	24-29%?	20%	posterior ?	no	525- 625	44-112	ż	ć	2
O. calamensis Puga & Formas, 2005	Telmatobius dankoi (Ceratophryidae)	Chile	34-60	20-38%	25- 50%	anterior- posterior	ou	225- 296	45-70	9 to 19 on each side	30-33	2
O. ceratophryos (Parodi & Widakowich, 1916)	Ceratophrys ornate (Ceratophryidae)	Argentina	ċ	16-20%	33% ?	ċ	no	700	380	16-20 on each side	23	-
O. ecuadorensis Dyer, 1986	Hyla geographica (Hylidae)	Ecuador	92-121	33%	ć	posterior	yes	370- 450	29	22-30 on each side	30	2
O. hernandezi (Flores-Barroeta, 1955)	Rana sp. (Ranidae)	Mexico	59-78	25%	17- 20%	posterior	no	850	ċ	21-32	5	
O. noei Wolffhügel, 1948	Calyptocephalella gayi (Calyptocephalellidae)	Chile	200-250	ć	ć	٠.	no	410- 580	420	70 on each side	22-25	7
O. olseni Dyer & Altig, 1977	Hyla geographica (Hylidae)	Ecuador	126-160	16%	50- 60%	posterior	no	395- 440	43	17-27 on each side	30.5	2
O. oumanskyi n. sp.	Lepidobatrachus laevis (Leptodactylidae)	Paraguay	85-119	20-26%	35- 61%	posterior- anterior	yes	350- 410	96-09	18-25 on each side	23-26	2

Abbreviations: RSCS = percent of the length of cirrus-sac in relation to the width of the proglottis; PGP = position of the genital pore (cirrus pore) as % of the proglottis length from the anterior margin: Vagina = position of the vagina in relation with the cirrus-sac; Testicular field = the testes are organized in one field or in two fields; Total length (mm) = the total length of the worm.

TABLE 2. Species of Ophiotaenia from amphibians, with data on the relative size of their ovary

Species	Host	Locality	Ovary ratio %
Ophiotaenia alessandrae			
Marsella & de Chambrier, 2008	Hypsiboas boans	Ecuador	5.6
O. alternans Riser, 1942	Amphiuma tridactylum	U.S.A.	4.8
O. amphiumae (Zeliff, 1932)	Amphiuma tridactylum	U.S.A.	6.8
O. bonariensis Szidat & Soria, 1954	Leptodactylus latrans	Argentina	6.9
O. bonneti de Chambrier,			
Coquille & Brooks, 2006	Lithobates vaillanti	Costa Rica	6.9
O. bufonis (Vigueras, 1942)	Bufo peltacephalus	Cuba	7.1
O. calamensis Pugas & Formas, 2005	Telmatobius dankoi	Chile	4.5
O. carpathica (Sharpilo, Kornyushin &			
Lisitsina, 1979)	Triturus cristatus	Ukraine	8.8
O. ceratophryos (Parodi & Widakowich,			
1916)	Ceratophrys ornata	Argentina	7.9
O. chandrae n. comb.	Duttaphrynus melanostictus	India	8.6
O. cryptobranchi La Rue, 1914	Cryptobranchus alleganiensis	U.S.A.	5.6
O. ecuadorensis Dyer, 1986	Hyla geographica	Ecuador	7.1
O. filaroides (La Rue, 1909)	Ambystoma tigrinum	U.S.A.	10.8
O. gracilis Jones, Cheng & Gillespie,			
1958	Rana catesbeiana	U.S.A.	7.9
O. hernandezi (Flores-Barroeta, 1955)	Rana sp.	Mexico	10.3
O. loennbergii (Fuhrmann, 1895)	Necturus maculosus	U.S.A.	5.5
O. magna Hannum, 1925	Rana catesbeiana	U.S.A.	5.4
O. niuginii (Schmidt, 1975)	Rana arfarki	Papua New Guir	nea 8.6
O. noei Wolffhugel, 1948	Calyptocephalella gayi	Chile	6.6
O. olor (Ingles, 1936)	Rana aurora	U.S.A.	7.4
O. olseni Dyer & Altig, 1977	Hyla geographica	Ecuador	6.5
O. oumanskyi n. sp.	Lepidobatrachus laevis	Paraguay	6.7
O. ranae Yamaguti, 1938	Rana nigromaculata	Japan	8.9
O. saphena Osler, 1931	Rana clamitans	U.S.A.	8.4
O. schultzei (Hungerbühler, 1910)	Pyxicephalus adspersus	South Africa	21.5?
O. tigrina (Woodland, 1925)	Hoplobatrachus tigerinus	India	8.8

7.2%) (*O. schultzei* was not considered because the drawings are not suitable for taking reliable data). In species of *Ophiotaenia* from reptiles from all parts of the World except Europe, the relative ovarian size is 1.5-6.7% (x = 3.4%; see table 1 in Ammann & de Chambrier, 2008 and table 2 in de Chambrier *et al.*, 2012).

Based on the new data and those of de Chambrier *et al.* (2012), it is possible to distinguish four groups in all spp. of *Ophiotaenia* and *Proteocephalus* (161 species): three for *Ophiotaenia* spp. and one for *Proteocephalus* spp. (i) 3 *Ophiotaenia* species, parasites of reptiles from western part of the Palaearctic region, with relative size of ovary 9.1-12.7% (x = 10.3%); (ii) 63 *Ophiotaenia* species, parasites of reptiles from all regions except for the Palaearctic Region, with relative size of ovary 1.5-6.7% (x = 3.4%); (iii) 25 *Ophiotaenia* species parasites of amphibians, with relative size of ovary 4.5%-10.8% (x = 7.2%); (iv) 70 *Proteocephalus* spp, parasites of teleost fishes from all regions, with relative size of ovary 5.4-20.2 (x = 11.9%) (*Proteocephalus midoriensis* Shimazu, 1990, with relative size of ovary of 28.8%, is not considered because the ovary illustrated does not seem to be of typical shape – see Shimazu, 1990, Fig. 12) (see table 1 in de Chambrier *et al.*, 2012).

These data show that the relative ovarian size of all known *Ophiotaenia* spp. from anurans is higher than those of reptilian hosts, but the number of species measured remains low and more information is needed.

As observed by de Chambrier *et al.* (2006), proteocephalidean cestodes are rare parasites of amphibians. In the Neotropical region (Costa Rica, Ecuador and Paraguay), these authors found cestodes in 11 of about 200 species of amphibians and prevalence was only 0.4% to 3.0% (de Chambrier *et al.*, 2006).

Proteocephalus bufonis Chandra & Gupta, 2007, a parasite of Bufo melano-stictus is preoccupied by Proteocephalus bufonis Vigueras, 1942 (Chandra & Gupta, 2007; Vigueras, 1942). Due to this homonymy, we propose Proteocephalus chandrae nom. nov. for P. bufonis Chandra & Gupta, 2007. Furthermore, this species shows the characters of Ophiotaenia, such as mature and gravid proglottides being markedly-longer than wide (see Freze, 1965) and thus is transferred to Ophiotaenia as Ophiotaenia chandrae n. comb.

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Corrigendum: *Draconectes narinosus*, a new genus and species of cave fish from an island of Halong Bay, Vietnam (Teleostei: Nemacheilidae)

by M. KOTTELAT, Revue suisse de Zoologie 119 (3): 341-349

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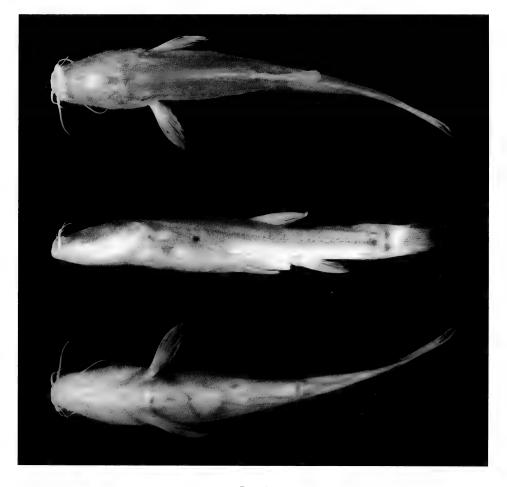


Fig. 1

Draconectes narinosus, MHNG 2730.080, 24.7 mm SL; Vietnam: Ha Long Bay: Dao Van Gio island, Dong Duc Tien cave; right side, reversed. Photographs by Tan Heok Hui.

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MERTEN'S, R. & WERMUTH, H. 1960. Die Amphibien und Reptilien Europas. Kramer, Frankfurt am Main, XI + 264 pp.

HANDLEY, C. O. JR 1996. Checklist of the mammals of Panama (pp. 753-795). *In*: Wenzel, R. L. & Tipton, V. J. (eds). Ectoparasites of Panama. *Field Museum of Natural History, Chicago*, XII + 861 pp.

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